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OBITUARY

Donald Strathearn Rawson

1905—1961

Doctor Donald Strathearn Rawson, a Member of the Fisheries Research Board of Canada, died suddenly and unexpectedly in Saskatoon on February 16, 1961.

Dr Rawson was born on May 19, 1905 near Uxbridge, Ontario, the son of Reuben Richardson and Mary (McFarlane) Rawson. He obtained his early education at Claremont and at Toronto's Harbord Collegiate Institute. Entering the University of Toronto in 1922, he received from it the degree of Bachelor of Arts in 1926, Master of Arts in 1927, and Doctor of Philosophy in 1929. His academic career was outstanding, and he was active in extra-curricular activities.

In 1932 Dr Rawson married Hildred Patton, who survives him, as do two sons and a daughter.

Dr Rawson was appointed in 1928 to the staff of the Department of Biology, University of Saskatchewan, and remained there through the remainder of his life, becoming head of the Department in 1949.

As an undergraduate and graduate student at Toronto Dr Rawson was a member of the Ontario Fisheries Research Laboratory, working first at the Lake Nipigon field station and other points in northern Ontario, later at Lake Simcoe. His Lake Simcoe studies concerned the bottom fauna of that lake and its role in fish production, providing material for both his M.A. and Ph.D. theses. These investigations, published in the University of Toronto Studies, Biological Series, were the first of his many contributions to Canadian limnology.

On arriving in Saskatchewan, Dr Rawson immediately undertook a survey of the lakes in the recently established Prince Albert National Park (1928–34). His recommendations formed the basis for rational utilization of the Park's fishing opportunities, and quickly led to requests for similar studies in other parts of western Canada. Among the surveys carried out by Dr Rawson or under his leadership may be mentioned the study of Paul, Okanagan and other lakes of interior British Columbia (1931, 1935); Clear Lake in Riding Mountain National Park, Manitoba (1935); the saline lakes of southern Saskatchewan (1938–41); lakes in the mountain parks of Alberta (1939, 1946, etc.); Lake Athabaska (1943 and 1945); Great Slave Lake (1944–47); Lac la Ronge, Reindeer Lake and other lakes in northern Saskatchewan (1948–58).

Almost without exception, these various surveys were requested with a view to obtaining a guide for best utilization of the waters concerned—either before a fishery began or because of dissatisfaction with an existing fishery. The results from this point of view have been published in such journals as the Canadian Fish Culturist, Transactions of the American Fisheries Society, the Bulletins and Journal of the Fisheries Research Board of Canada, and Fisheries Reports of the Saskatchewan Department of Natural Resources. Best known perhaps is the Great Slave Lake Survey sponsored by the Fisheries Research Board, which set the stage for commercial exploitation of that lake and for a continuing study of its fish production.

The development of fisheries management in Saskatchewan was largely influenced by Dr Rawson's investigations. His wide knowledge of the prairie

lakes made him a leader among the five members of the Royal Commission on the Fisheries of Saskatchewan in 1946–47. In recent years he encouraged the growth and development of a Provincial Fisheries Research Laboratory with headquarters at the University of Saskatchewan, which has continued the work of sound appraisal as a basis for management.

During all these studies Dr Rawson and his colleagues gave detailed attention to the physical characteristics and biological populations of the waters examined. Their publications concerning various facets of the life and environment of Lake Waskesiu, Prince Albert Park, have made that lake a classical locality among limnologists. Furthermore, broad acquaintance with different lake types in many regions stimulated Dr Rawson to publish a number of studies in which different types are compared and contrasted. These analyses are his most important scientific works for they deal with the fundamental problems of relating physical characters of morphometry, climate and geology to the production of plants and animals in lakes.

In 1944 Dr Rawson was elected a Fellow of the Royal Society of Canada. He was appointed as a member of the Fisheries Research Board in 1959, after being for many years an influential adviser of many of its activities.

Dr Rawson was a member of the American Association for the Advancement of Science, American Society of Ichthyologists and Herpetologists, American Fisheries Society, and Ecological Society of America. He was one of the founders of the Limnological Society of America (now the American Society of Limnology and Oceanography) and served as its President in 1947. At the time of his death and for many years previously he had been Canadian representative on the Council of the International Association for Theoretical and Applied Limnology. During 1936–46 he was a member of the National Committee on Fish Culture, and subsequently of the informal Canadian Committee for Freshwater Fisheries Research, of which he was President in 1951. He assisted with the organization of the Canadian Conservation Association, and later of the Canadian Society of Wildlife and Fishery Biologists, which in one of its aspects can be considered the Association's successor.

Enthusiasm for research did not prevent Dr Rawson from maintaining a steady teaching schedule at the University. He also contributed in many ways to student activities, particularly athletics, and, in later years he assumed the cares of supervising a large university department. His wife and children were his greatest pride, but he gave to his students an almost equal measure of devotion. He was intensely interested in biologists in training, and followed their subsequent careers with an active and sympathetic correspondence. His numerous graduate students occupy positions in research, teaching and fishery management throughout Canada and abroad. In recent years the planning and construction of a new biology building on the Saskatoon campus of the University of Saskatchewan took much of his time: this beautiful and functional building is an enduring monument to his labours.

Proximate Composition of Canadian Atlantic Fish
I. Variation in Composition of Different Sections of the Flesh of Atlantic Halibut (*Hippoglossus hippoglossus*)[1]

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ABSTRACT

The composition of various portions of the edible flesh of Atlantic halibut (*Hippoglossus hippoglossus*) varies greatly, especially in lipid content. The muscle of the belly flap and the dark muscle along the lateral lines in the upper and lower sides have a high lipid content, 2.4 to 9.7%, with correspondingly lower moisture content, about 68 to 75%, and a slightly low protein content, about 16.3 to 19% (protein N × 6.25) in comparison with the light meat. The latter, which makes up the larger part of the edible tissue, nearly 90%, ranges from 0.9 to 1.4% lipid, 75 to 77% moisture and 17.5 to 20.3% protein. These values are almost identical to those for Pacific halibut (*Hippoglossus stenolepis*). Non-protein nitrogenous extractives are also lower in the white meat.

The figures most often quoted in nutritional tables for the lipid content of halibut (5 to 6%) are probably much too high for the portions usually eaten, which average about 1.2% for the white meat, and about 1.5% if the dark meat is included.

INTRODUCTION

It has been recognized for many years that the composition of the edible portion of the flesh of fish and shellfish varies with many factors, among them, size, sex and stage of sexual maturity, season and place of catching. Atwater (1892) concluded that there was some seasonal influence in certain species, as during the spawning migration of salmon. Clark and Almy (1918) found large variations in fat content with feeding activity and with the spawning cycle, particularly in shad. Johnstone (1918) studied the maturation of herring showing the accompanying large changes in fat and moisture. Thus, abundance of food, spawning cycle, spawning migrations and age influence the composition of any particular species. The effect of these factors has been reviewed recently by Stansby (1954) and Vinogradov (1953).

Tables of proximate composition of the edible portion are given in several reference works, e.g. McCance and Widdowson (1940), Watt and Merrill (1950), but usually few data are given on the number of samples analyzed, and indeed it is known that many quoted figures are based on single determinations.

It is only recently that the variation in different parts of the muscle from an individual fish has been emphasized (Brandes and Dietrich, 1953; Thurston, 1958; Thurston and MacMaster, 1960) although it was recognized by Clark and Clough (1926) in certain fatty species.

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The major constituents are water, fat, and protein, with ash and certain extractives including non-protein nitrogenous compounds making up lesser amounts. In general, the moisture content is about 80% with reduced levels in the more fatty species. The protein content has been found to remain relatively constant except under conditions of advanced starvation, in spite of great variations in fat content. This is usually expressed by the rule that the sum of the percentages of water and fat is nearly constant, about 81% (Clark and Almy, 1918). For instance, in herring (*Clupea harengus*) Reay *et al.* (1943) found that the percentage of water was equal to 80.2 – (0.96 × percentage of fat).

The ash content usually varies between 1 and 1.5%. Higher values usually indicate inclusion of bone or sometimes brining prior to sampling.

The procedures often used for fat and lipid determination have yielded results dependent on the solvent and procedure (Love *et al.*, 1959). The development of two apparently more reproducible procedures should lead to the resolution of this difficulty (Dambergs, 1956; Bligh and Dyer, 1959).

There is a real scarcity of data on the composition of the Canadian Atlantic species, its variation in different parts of the fillet or individual fish, and the effect of the various processing and preservation procedures. It is evident that such data are of interest to dietitians concerned with nutritional values of fish and sometimes with levels of fat and salt in the diet, and to processing engineers who deal with the varying yields of primary products, with the various by-products in all seasons and with fish from various sources.

A study was thus undertaken of some Atlantic species of fish and shellfish, of which this report on Atlantic halibut (*Hippoglossus hippoglossus*) is the first part.

METHODS

1. Sampling

In small halibut (chicken halibut) a cross-sectional slice was taken from the thickest part of the fish, following the practice of Love (1958, 1960) who used the region from myotome 7 to 14 which in cod is about one-quarter along the length of the fillet from the anterior end. This was designated A, and another was taken from the tail section about half-way between the vent and the end of the fillet, designated B.

Another sample was taken from the thin section of muscle around the abdominal cavity, designated the belly flap, C.

In large halibut, steaks were obtained from about the same regions as A and B above, but in this instance, three samples were cut from each steak: the upper one-eighth portion of the steak, D; the lower one-eighth portion, F; and the central portion, E. (See diagram, Fig. 1.) Thus the fatty layer running along the centre of each side was removed, leaving the relatively lean white muscle in the central part (E). Somewhat the same procedure with some additional sampling was used by Thurston and MacMaster (1960), published after this work was completed. Thus samples D and F contained a small proportion of white meat in addition to the fatty layer. The skin and bones were carefully removed in all

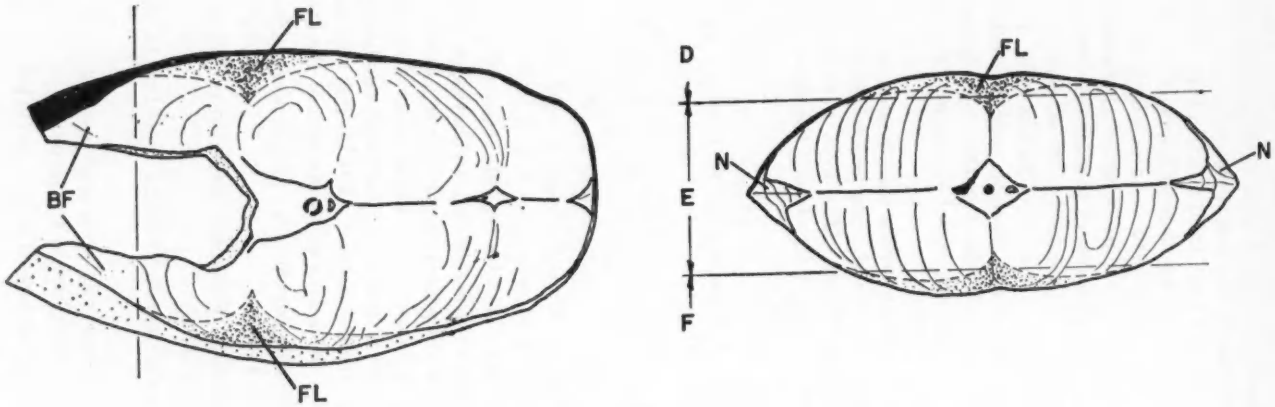

FIG. 1. Diagram of halibut steak showing sampling locations:
FL—Lateral dark muscle;
BF—Belly flap;
D—Upper section of tail steak;
F—Lower section of tail steak;
E—Central section of tail steak;
N—"Notch" meat around dorsal and ventral fins.

samples. The samples were then comminuted with a knife, well mixed, and portions weighed immediately for the various analyses.

The halibut were obtained iced fresh from a local plant. They were caught by shore boats in local waters and were less than 24 hours in ice. Dates of landing are given in the Tables. In one instance steaks from a large halibut were frozen and stored in polyethylene bags at −23°C for a period of 2 months.

To determine the relative proportion of white meat, etc., frozen steaks from a medium halibut, about 100 lb, were obtained. These were frozen samples of unknown age but in good condition. The skin, dark muscle, white muscle and bone which readily separated on partial thawing were carefully dissected out, weighed and analyzed. In addition, the "notches" or wedges of whitish, jelly-like tissue, N in Fig. 1, in which the dorsal and ventral fins were embedded, were also separated.

Two samples of "chalky" halibut, which were landed at a local fish plant from a trawler, were examined. The flesh appeared to be quite opaque, flaked apart easily, was softened and very wet. The light meat only from a cross-sectional "steak" cut from the thickest part of each fish was analyzed.

2. Analytical Methods

Water. Samples of 20 to 50 g were dried to constant weight at 105°C, usually for 24 to 48 hr.

Lipid. Samples of 50 g were extracted according to the chloroform–methanol phase separation procedure of Bligh and Dyer (1959).

Ash. Samples were ignited to constant weight at 550°C.

Total nitrogen (TN). The Kjeldahl–Gunning–Arnold method (A.O.A.C., 1955) was employed, using 2- to 5-g samples.

Non-protein nitrogen (NPN). A 25-g sample was triturated with trichloroacetic acid of a final concentration of 5%, and nitrogen was determined in the filtrate using a micro-Kjeldahl procedure (Dyer *et al.*, 1950).

Certain non-protein nitrogenous constituents were also determined to indicate whether these constituents varied in the same manner as the major constituents. The content of trimethylamine (TMA) and ammonia, and the tyrosine value, also served as a check on the "freshness" of the samples.

TMA. Aliquots of the trichloroacetic acid filtrate were subjected to the colorimetric procedure of Dyer (1959).

Trimethylamine oxide (TMAO). Following reduction to TMA (Dyer *et al.*, 1952) the latter was estimated as above.

Tyrosine. The tyrosine value was determined according to the procedure of Wood *et al.* (1942).

Ammonia. One gram of tissue was triturated with 200 ml water and ammonia estimated in the filtrate with Nessler's reagent.

Free fatty acid (FFA) The procedure of Bligh *et al.* (1957) was employed.

Salt-extractable protein N (SPN) *and actomyosin* N (AM). Samples of 22.5 g were blended with 0.85*M* NaCl (0.003*M* bicarbonate buffer) for 2.5 minutes (Dyer *et al.*, 1950).

RESULTS AND DISCUSSION

In chicken halibut, about 2½ ft in length, differences appear in moisture and lipid content between samples taken from the thick section and from the tail (Table I). The thick section averages 3.1% lipid, in comparison with only 1.2% in the section toward the tail, while the belly section has much more, 4.8%. As expected, the moisture content of the latter is less than in the cross-section samples. It is apparent that some fatty meat from the belly section and from the fatty strip running down each side is being included in the cross-section samples. Consequently in subsequent sampling these fatty tissues were removed, leaving the apparently fatty-tissue-free central section. The belly flap has a slightly lower protein content, 15.6% expressed as protein nitrogen × 6.25, with a higher proportion of total nitrogen present as NPN (Table II). However, the TMAO level is the same for all sections.

The results for the three samples of large halibut show that a large part of the fat is concentrated along the "lateral lines". The upper section (D) contains from 2.4 to 9.1% lipid, the lower (F) 3 to 9.9%, while the central section has only 0.9 to 1.4%. Moisture contents are correspondingly less in the more fatty sections where NPN is higher and protein lower. Again there is little change in TMAO. The constancy of the TMAO content is interesting since Shewan (1951) indicates that the dark muscle of herring and tunny contains only half as much as the rest of the skeletal muscle. Tyrosine values are higher in the fatty layers, probably indicating more soluble peptides and amino acids.

For convenient comparison with earlier literature, the sum of moisture, ash, lipid, and crude protein (TN × 6.25) is given in Table I. Since at least some of the NPN may be used for protein synthesis in metabolism, this method of calculating results may have some usefulness, e.g. for dietetic purposes, especially since it is the most commonly used procedure. (For a more complete discussion, see Vinogradov (1953) and Love (1957).)

The sum of moisture, lipid, ash, and protein nitrogen × 6.25 is also given. It does not include the non-protein nitrogenous compounds or other extractives, and therefore the sum usually adds to about 97%. This was partially allowed for in the earlier literature by calculating protein as total nitrogen multiplied by the factor 6.25. It seems better to calculate true protein (assuming nitrogen content of muscle protein is 16.0%), and the differences between the sum obtained and 100 will then give a rough measure of the extractives, which, from the average of all values given, is about 2.5%. In cod, the nitrogenous extractives consist mainly of creatine, trimethylamine oxide, taurine, anserine, purine and pyrimidine derivatives (Shewan and Jones, 1957). For the composition given by these authors, the average nitrogen content of these nitrogenous extractives is 21%. Since the nitrogenous extractives from cod and the flatfishes are quite similar

TABLE I. Proximate composition—percent wet weight.

Data		Water	Lipid	Ash	TN	Crude protein[3]	Total A[4]	NPN	PN[5]	Protein[6]	Total B[7]
Chicken halibut	A1	74.5	3.1	1.35	3.38	21.1	100.0	0.57	2.81	17.5	96.5
(Feb. 9, 1959)	A2	76.1		1.38	3.37	21.1	101.7	0.57	2.80	17.5	98.1
2 fish	B1	77.2	1.2	1.50	3.38	21.1	101.0	0.70	2.68	16.8	96.7
	B2	76.9		1.55	3.36	21.0	100.6	0.71	2.65	16.6	96.3
	C1, C2	75.9	4.8	1.53	3.28	20.5	102.7	0.79	2.49	15.6	97.8
Large halibut	D	70.4	9.1	1.20	3.43	21.4	102.1	0.55	2.88	18.0	98.7
(June 6, 1959)	E	76.2	1.4	1.25	3.66	22.9	101.7	0.43	3.24	20.2	99.1
Tail steak	F	69.2	9.4	1.15	3.41	21.3	101.0	0.54	2.88	18.0	97.8
Large halibut (July 24, 1959)	D	75.5	2.4	1.40	3.31	20.7	100.0	0.71	2.60	16.3	95.6
Steak from back of vent	E	77.6	0.9	1.30	3.26	20.4	100.2	0.46	2.80	17.5	97.3
	F	74.1	3.0	1.30	3.47	21.7	100.1	0.73	2.74	17.1	95.5
Large halibut (Apr. 20, 1959)	D	72.4	6.9	1.30	3.49	21.8	102.4	0.48	3.01	18.8	99.4
Steak from back of vent frozen	E	75.1	1.2	1.45	3.63	22.7	100.4	0.38	3.25	20.3	98.1
and stored 2 mo. at −23°C	F	68.0	9.9	1.00	3.41	21.3	100.2	0.55	2.86	17.9	96.8
Chalky halibut	A1	78.8	1.1	1.40	3.16	19.7	101.0	0.51	2.65	16.6	97.9
Light meat only from Section A	A2	76.4	0.9	1.30	3.56	22.2	100.8	0.51	3.05	19.0	97.7
Average E (3)		76.3	1.2	1.33	3.51	21.9	...	0.42	3.09	19.3	...
Average D + F		71.6	6.8	1.27	3.42	21.4	...	0.59	2.83	17.7	...

[3]Crude protein—TN × 6.25.
[4]Total A—Sum of water, lipid, ash and crude protein.
[5]PN—Protein N
[6]Protein—PN × 6.25.
[7]Total B—Sum of water, lipid, ash and protein.

TABLE II. Non-protein nitrogenous and protein constituents.

Data		NPN	NPN	TMA	TMAO	NH_3	Tyr.	SPN[8]	AM[9]	Alb[10]	FFA[11]
		% wet weight	*%TN*	*mg N/100 g*				*% TPN*[12]			*% lipid*
Chicken halibut	A1	0.57	16.8	0.24	46	...	...	...	...	...	2.7
(Feb. 9, 1959)	A2	0.57	16.9	0.25	47	...	...	...	...	...	...
2 fish	B1	0.70	20.7	0.24	46	...	...	...	...	...	4
	B2	0.71	21.1	0.21	47	...	...	...	...	...	...
	C1, C2	0.79	24.0	0.24	46	...	...	...	...	...	1
Large halibut	D	0.55	16.0	1.9	56	14	38	60	42	18	0.6
(June 6, 1959)	E	0.43	11.5	0.4	59	8	18	76	53	22	1.6
Tail steak	F	0.53	15.5	0.6	58	14	56	65	42	23	0.4
Large halibut	D	0.71	21.4	2.2	57	14	49	81	55	26	2
(July 24, 1959)	E	0.46	14.1	1.3	63	17	24	86	62	24	4
Steak from back of vent	F	0.73	21.0	2.2	58	17	87	71	47	24	1.5
Large halibut (Apr. 20, 1959)	D	0.48	13.8	0.6	54	9	29	71	49	22	3
Steak from back of vent	E	0.38	10.3	0.4	57	12	17	78	54	24	9
frozen and stored 2 mo. at −23°C	F	0.55	16.1	0.5	50	12	46	68	45	23	3
Chalky halibut (May 1, 1959)	A1	0.51	16.2	0.7	68	...	...	82	62	20	7
Light meat only from Section A	A2	0.51	14.3	0.8	65	...	...	55	40	15	12
Average E (3)		0.42	12.0	0.7	60	...	...	80	...	23	...
Average D + F		0.59	17.3	1.3	55	...	...	70	...	23	...

[8]TPN—Total protein N.
[9]SPN—Salt-extractable protein N.
[10]AM—Actomyosin N.
[11]Alb—Albumin N.
[12]FFA—Free fatty acid.

both in kind (Shewan, 1955), and in amount (Shewan, 1951), we can calculate that the total nitrogenous extractives in the white flesh of the halibut will be approximately 2.0% using a NPN content of 0.42%

Allowing for a smaller amount of non-nitrogenous extractives, the total proximate composition is thus close to 100%.

The average values for the three central (E) sections and combined upper and lower (D and F) sections are shown at the bottom of the Tables and illustrate the differences between the fatty tissue and the white muscle.

It is interesting to compare these averages with the data of Thurston and MacMaster (1960). For small and large specimens of the closely related Pacific halibut (*Hippoglossus stenolepis*), the average of the nape, central and tail sections (which showed almost no differences between them), excluding the belly flaps and dark muscle, was 77.9% moisture, 0.7% lipid, 1.39% ash, and 21.2% crude protein. The corresponding averages obtained in the present work, sample E, were 76.3, 1.2, 1.33 and 22.0% respectively. This agreement appears to be remarkable indeed. The higher average lipid content could be due to the different procedure used for its estimation. These authors also found a high lipid content averaging 7% in the fatty brownish layer which corresponds with the high value, 6.8%, in the D and F samples in the present work.

Several authors quote data for the composition of the muscle tissue of halibut (mainly *Hippoglossus hippoglossus*) e.g.:

	Water	*Fat*	*Crude protein*	*Ash*
Reay *et al.* (1943)	75.4–79.0	0.5–9.6	18–18.8	. . .
Taarland *et al.* (1958)	74.5	6.0	18	1.0
Watt and Merrill (1950)	75.4	5.2	18.6	1.0
Vinogradov (1953)	74.5–77.6	. . .	18.1–20.5	0.7–1.1

It will be seen that with the exception of fat, these values are close to the present results , although ash and crude protein are slightly lower.

The figures quoted for fat content are rather high, and are close to the values obtained for the fatty tissue in the present work. Perhaps nutritionists and dietitians would be well advised to use the much lower values of the white meat, about 1.2%, since this is the portion which will be eaten by most people, the more fatty portions often being discarded prior to serving, or left on the plate.

The proportion of the total nitrogen contributed by NPN is remarkably higher for the fatty upper and lower sections, 17.3%, than for the central section, 12%. NPN was not determined by Thurston and MacMaster. Lukton and Olcott (1958) give a NPN content of 0.38% for the Pacific halibut, very close to the present results.

The proportion of the edible flesh in the steaks from both the thick section of the fish and from the tail section was the same, 91.0 and 90.5% respectively (Table III). The skin was 3.4% in both cases, bone constituting the remainder. Of the edible portion the white meat constituted about 90%, the dark or fatty layered meat 6 to 7%, and the "notch" meat 3.6 to 5.2%.

TABLE III. Proportion of skin, bone and edible meat in halibut steaks (frozen halibut steaks, December 1960).

	Steak from thickest section of fish (Section A) (Total wt. 735 g)	Steak from tail section (Section B) (Total wt. 408 g)
Proportion of total weight represented by:		
Skin	3.4	3.4
Bones	5.6	6.1
Edible portion	91.0	90.5
Proportion of edible weight represented by:		
White meat	90.2	87.4
Dark meat (FL)	6.2	7.4
Notch meat	3.6	5.2

The analytical data for these portions (Table IV) agree closely with the results already reported. The white meat contains only 0.74 to 1.14% lipid as compared to 3.9 to 8.5% for the dark meat. The steaks were not taken from the same fish so no comparison of the tail and middle steaks can be made in this case. If the average fat of the edible portion is calculated, taking into account the lipid content and the proportion of each type of meat, the middle steak averages 1.7%, and the tail steak, 1.3% These data support the conclusion that the usual fat content quoted for halibut is much too high.

TABLE IV. Composition of white and dark meat of halibut steak (from samples used in Table III).

	Water	Lipid	TN	Crude protein	NPN	PN	Protein	NPN % TN	TMA	TMAO
	% wet weight								*mg N/100 g*	
Middle steak—A										
White meat	77.2	1.14	3.23	20.1	0.46	2.79	17.3	14.2	0.2	69
Dark meat	71.7	8.5	3.00	18.8	0.55	2.45	15.3	18.3	1.3	54
Tail steak—B										
White meat	79.9	0.74	3.04	19.0	0.43	2.61	16.3	14.1	0.2	70
Dark meat	76.9	3.9	2.88	18.0	0.63	2.25	14.1	21.9	2.6	53
Notch meat	76.6	7.6								

NPN is considerably higher in the dark meat, while on the other hand the TMAO content is about 23% lower. The lipid content of the "notch" meat is high, 7.6%, even though this portion is almost colourless to white, being non-pigmented in sharp contrast to the brownish fatty layer along the lateral lines. The sample analyzed was lower in fat than the corresponding portion of the Pacific halibut which is reported to contain about 40% fat (Thurston and MacMaster, 1960).

In the chalky halibut the lipid content is normal, 0.9 to 1.1%. Moisture and protein are normal in one sample, although protein is considerably lower in the other, only 16.6%.

The protein extractable in neutral 0.85*M* sodium chloride solution was determined on several of the samples (Table II). The E samples average approximately 80% (as percentage of total protein nitrogen). This value is rather low when compared to most values for fish flesh, and probably more could be obtained by more exhaustive extraction. However, on a comparative basis, that extracted from the D and F samples is considerably lower, averaging 70%. The albumin or water-soluble protein, that fraction remaining after precipitation of the actomyosin from the salt extracts by dilution to an ionic strength of 0.05, averages 23% in both instances. The chalky halibut sample (A1), with rather low protein N content (2.65%), gives similar values, but the other (A2), containing 3.05% protein N, yields only 55% SPN and the albumin is also low, only 15%. The significance of these results is unknown, though there may be some relation to the spawning cycle when the depot fat and some of the body protein may be used to supply energy and protein to the rapidly increasing egg mass during maturation, in which case some of the protein may be replaced by water. In jellied plaice, Templeman and Andrews (1956) found much higher moisture than the normal, and much lower total protein and extractable actomyosin, while the proportion of unextractable or stroma protein was increased. The latter would result if muscle protein was depleted. The chalky halibut described here seems to be different from Pacific chalky halibut which appear to contain less water, more fat, and usually less protein (Bailey, 1950, 1951).

The present results show the great variation in lipid content in Atlantic halibut between the white meat of the central muscle, the dark meat along the sides, and the muscle of the belly flap. They are in substantial agreement with the extensive data of Thurston and MacMaster on the Pacific halibut.

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Proximate Composition of Canadian Atlantic Fish
II. Mackerel, Tuna and Swordfish[1]

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ABSTRACT

Mackerel, tuna and swordfish (order Acanthopteri) have a prominent red or dark brown fatty lateral-line tissue which, in the samples analyzed, had a lipid content varying from 6% in swordfish to 22% in mackerel. A white blubber or layer of fat tissue, almost two-thirds lipid, may also be present beneath the skin. The white meat was also fatty, from 2% in swordfish to 8% in tuna. The belly-flap muscle of mackerel contained from about 20 to 40% fat. Protein, ash and moisture percentages were lower in the fatty tissue, showing that fat replaces some protein as well as water. Non-protein nitrogen averaged 20% of the total nitrogen, higher than in halibut and the cod family. In tuna and mackerel the protein content was 19% in the white meat and 14% in the brown lateral-line tissue, similar to halibut but higher than in the cod family.

INTRODUCTION

In part I of this series (Mannan *et al.*, 1961) considerable differences in composition between various sections of the flesh of Atlantic halibut (*Hippoglossus hippoglossus*) were noted.

Some variations found in the composition of the various portions of the flesh of mackerel (*Scomber scombrus*), tuna (*Thunnus thynnus*) and swordfish (*Xiphias gladius*), all of the order Acanthopteri, are reported here. These species are characterized by the presence of a very prominent lateral-line muscle, usually of a red or dark brown colour. The importance of considering this section of the flesh separately is pointed out by Hamoir (1953a), who also shows that myoglobin is responsible for the red colour (1953b). This muscle in mackerel, herring and halibut has a very high fat content, 27 to 29% (Braekkan, 1956). Love *et al.* (1959) summarize the few data available on the composition of the dark meat of several fish species, showing that this part of the musculature is considerably different in some respects from the white muscle.

EXPERIMENTAL

Sampling and Source of Specimens

The iced fish were landed from small boats at a local fish plant, and were almost always less than 24 hr out of the water when sampled.

The fall mackerel samples were frozen and stored in polyethylene bags at −23°C for 3 months. As described in Part 1 of this series, cross-sectional samples were taken of the edible flesh near the thickest part of the fish, A, toward

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TABLE I. Composition of various sections of Atlantic mackerel, tuna and swordfish. (Crude protein is 6.25 × TN; total A is sum of water, lipid, ash, and crude protein; protein is 6.25 × protein nitrogen (PN); total B is sum of water, lipid, ash and protein.) (A, B, C, and DB refer to the sections of flesh from the thick part, tail, belly flap and lateral line, respectively (see text) P_1 and P_2, etc. refer to samples from different specimens of tuna and swordfish.)

		Water	Lipid	Ash	TN	Crude protein	Total A	NPN	PN	Protein	Total B	TMA	TMAO	SPN	Am.	Alb.	FFA	NPN
		Percentage of wet weight										*mg N/100 g*		*% TNP*			*% lipid*	*% TN*
Mackerel																		
(Dec. 9/58)	A	63.2	18.8	1.36	3.42	21.4	104.8	...	...	...	...	...	...	...	...	...	0.6	...
Frozen (−23°C)	B	65.3	12.6	1.41	3.60	22.5	101.8	...	...	...	...	...	...	...	...	...	5.4	...
3 mo.	C	49.3	37.2	0.99	2.60	16.3	103.8	...	...	...	...	...	...	...	...	...	0.5	...
(June 8/59)	A	74.4	3.2	1.64	3.67	22.9	102.1	0.62	3.05	19.1	98.3	0.4	39	94	72	22	1.4	16.9
Fresh—	B	74.0	4.9	1.50	3.57	22.3	102.7	0.54	3.03	18.9	99.3	0.3	39	95	74	21	1.7	15.2
Av. of 6	C	60.2	18.8	1.27	3.12	19.5	99.8	0.62	2.50	15.6	95.9	0.4	27	86	63	23	0.5	19.9
Specimens	DB	59.7	22.1	0.99	2.63	16.4	99.2	0.53	2.10	13.1	95.9	1.3	55	...	...	...	1.7	20.1
Tuna																		
(July 24/59)	P_1	71.1	6.9	1.15	3.79	23.7	102.8	0.72	3.07	19.2	98.4	1.1	10.5	90	61	29	0.4	19.0
Fresh	P_2	74.0	4.5	1.25	3.86	24.1	103.8	0.73	3.13	19.6	99.3	1.3	11.2	97	63	34	0.4	18.8
(Aug. 13/59)	P_1	68.2	8.2	1.20	3.92	24.5	102.1	0.75	3.17	19.8	97.4	1.8	12	96	65	31	0.4	19.2
Fresh	P_2	72.1	6.5	1.10	3.80	23.7	103.4	0.74	3.06	19.1	98.8	1.7	12	97	68	29	0.6	19.5
	F_1	46.8	34.5	0.80	2.92	18.2	100.3	0.68	2.24	14.0	96.1	3.6	9	97	62	35	0.2	23.1
	F_2	47.1	34.2	0.80	2.92	18.2	100.3	0.66	2.26	14.1	96.2	3.4	9	95	62	33	0.2	22.7
Blubber		...	64	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Swordfish																		
(July 24/59)	A_1	76.0	2.1	1.90	3.33	20.8	100.8	0.67	2.66	16.6	96.6	0.7	33	93	69	24	1.4	20.2
Fresh	A_2	76.6	1.9	1.90	3.32	20.7	101.1	0.68	2.64	16.5	96.9	0.8	32	97	75	22	1.7	20.5
	DB_1	74.9	6.3	1.20	2.97	18.6	101.0	0.71	2.26	14.1	96.5	2.1	29	97	71	25	3.4	22.9
	DB_2	74.4	6.5	1.25	2.97	18.6	100.7	0.70	2.27	14.2	96.4	2.3	30	97	72	25	3.5	23.6

the tail, B, and of the flesh of the belly flap, C. In the June 8 samples, the dark brown muscle (DB) along the lateral line (FL, fig. 1 in Part 1) was analyzed separately. The flesh of six specimens was minced and well mixed for these samples. In tuna samples of the pink (white) meat (P), the whitish fatty meat which was layered somewhat like bacon (F), and the thick layer of blubber under the skin were taken.

In the swordfish the white (A) and dark (DB) meat from steaks near the middle section were sampled.

The analytical procedures used are given in Part 1 of this series. All values given in Table I for total nitrogen (TN), non-protein nitrogen (NPN), trimethylamine oxide (TMAO), trimethylamine (TMA), salt-extractable protein nitrogen (SPN) and actomyosin nitrogen (AM) are the average of duplicate determinations.

RESULTS

These species have high fat levels in the muscle tissue. The fat fall mackerel specimens have lower lipid in the tail section (12.6%) than in the thick part (18.8%), while the fat in the belly flap is much higher, 37.2%. The spring mackerel (June 8) with a much lower total fat content still retains 18 to 19% fat in the belly flap, 4 to 6 times the content of the white flesh. The dark brown muscle of the lateral line comprises 1/7 of the weight of the edible flesh. The proportion of dark muscle is greater in the tail section, 27%, as compared to 11% in the thick section (Table II). The dark muscle also has a high fat content,

TABLE II. Proportion of skin, bone, and edible meat in steaks of fall mackerel. Fish 34 cm long.

	Steak from thickest part of fish (Section A) (Total wt. 155 g)	Steak from tail section (Section B) (Total wt. 68 g)
Proportion of total weight represented by:	%	%
Skin	3.0	2.7
Bone	5.6	10.7
Edible portion	91.4	86.6
Proportion of edible portion represented by:		
White meat	71	73
Dark layer	11.3	27
Belly flap	18.5	0

about 22%. Moisture, ash and protein are lower in the brown fatty lateral line and belly flap tissue, while TMAO is higher in the brown layer.

Tuna has rather more fat in the pink muscle, 4 to 8% (mackerel, 3.2 to 4.9%), while the thick layer of whitish fatty meat is much fattier, 34% (mackerel 18.8%). A sample of blubber from near the skin shows 64% fat. Protein levels are considerably lower in the fatty tissues.

The swordfish samples are less fatty, the levels averaging 2 and 6% in the white and dark meat respectively. The NPN constituents are almost identical but protein, ash and moisture are lower in the dark meat.

The NPN levels in this group are considerably higher than in the halibut and cod families, averaging about 20% of the total nitrogen. In swordfish, a much lower value of 0.24% NPN is reported by Lukton and Olcott (1958). The TMAO levels are quite low in this group in agreement with previous work (Groninger, 1959).

The protein (protein N × 6.25) of the white meat, 16.5 to 18.8%, is similar to halibut and somewhat higher than in the cod family. The fat tissue, however, contains only about 14%. The protein extractability in salt solution is comparable to the other groups, varying from 90 to 97% extractable protein nitrogen, with slightly lower values in the dark brown muscle of the mackerel. The albumin fraction is considerably higher in the tuna, about 32% of the protein as compared to about 23% in other fish species.

The free fatty acid (FFA) of the extracted fat is very low, probably because of the high fat levels. Even in mackerel frozen at −10°F for 3 months, there was no appreciable hydrolysis of the fat.

In Table III some published values for the proximate composition of these species are tabulated. Apart from wide variations in moisture and especially lipid content associated with seasonal changes, the protein and ash are quite constant and consistent with our results when the variations due to sampling such a mixture of lean and of fatty tissue is considered. The distinguishing characteristic of this group of fishes is the presence of a variable and often large

TABLE III. Proximate composition of edible flesh of mackerel, tuna and swordfish.

Source	Water	Lipid	Ash	Crude protein (total nitrogen ×6.25)
	Percentage of wet weight			
Mackerel (*Scomber scombrus*)				
Watt and Merrill (1950)	68.1	12.0	1.2	18.7
Vinogradov (1953), (Av. of 11)	70.0	. . .	1.36	19.6
Range:	64.4–73.1	. . .	0.9–1.85	15.6–24
Braekkan and Probst (1953)	74.0	5.1	1.3	19.6
Taarland *et al.* (1958)–Spring	74.3	5.4	1.5	18.6
–Fall	60	20.2	1.3	18.5
Tuna (*Thunnus thynnus*)				
Dill (1921)	65–73	1–9	1.3–1.4	24–25
Vinogradov (1953), (Av. of 3)	70.2	. . .	1.3	26.5
Range:	69.1–70.8	. . .	1.25–1.4	26.5
Taarland *et al.* (1958)	66.0	9.9	1.1	24
Swordfish (*Xiphias gladius*)				
Lopez-Matas and Fellers (1948)	76.6	3.1	1.0	18.9
Watt and Merrill (1950)	75.8	4.0	1.3	19.2
Vinogradov (1953), (Av. of 4)	76.6	. . .	1.4	19.8
Range:	75.3–77.5	. . .	1.2–1.5	18–20.5

proportion of the brown fatty lateral-line tissue. In some species there is present a layer of depot fat or blubber below the skin which is about two-thirds fat. The latter may correspond to the white fatty "notch" meat in halibut. The contrast with the lean fishes of the cod family is striking, lipid being much higher, and it was found that the protein and NPN contents are also greater. This higher content of NPN contributes to and enhances the flavour of these species (Shewan, 1951).

The large differences in the composition of the various tissues in these species make sampling for detection of storage changes and accurate determination of composition for dietetic and other purposes extremely difficult.

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The Amino Acid Composition of Cod Tropomyosin[1]

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ABSTRACT

The amino acid composition of cod tropomyosin was determined. Most analyses were done by chromatography on columns of ion-exchange resins (Moore and Stein technique); tryptophan and cystine were determined chemically.

The results are compared with published values for tropomyosins from other sources. Similarities and differences between the various tropomyosins are discussed. The probable number of residues of each of the amino acids in the tropomyosin molecule is calculated.

INTRODUCTION

Following Bailey's (1946, 1948) discovery of tropomyosin as a protein component of rabbit skeletal muscle, many have studied the chemical and physical properties of this protein. The earlier investigations (Astbury, 1947; Bailey, 1948; Bailey *et al.*, 1948; Astbury *et al.*, 1948; Adair *et al.*, 1949) were mainly concerned with tropomyosin from rabbit muscle. Hamoir's (1951) was the first publication dealing with tropomyosin from another species of animal; it described the isolation of the protein from carp muscle. Since then, tropomyosins from many additional animals have been studied: squid (Yoshimura, 1955); pig, duck, prawn, cuttlefish (Tsao *et al.*, 1955); *Pinna nobilis* (Bailey, 1956); octopus, oyster (Bailey, 1957); clam (Laki, 1957); cow, man (Kominz *et al.*, 1957c); lobster, whelk, lugworm, earthworm (Kominz *et al.*, 1957a, b); haddock (Kubo, 1957); scallop (Rüegg, 1958); lamprey, frog (Saad *et al.*, 1959); and cod (Dingle and Odense, 1959).

It now appears that at least two tropomyosins exist, commonly referred to as "vertebrate" and "invertebrate" types, with different solubilities in ammonium sulphate solutions (Bailey, 1948, 1956, 1957; Bailey and Rüegg, 1960; Kominz *et al.*, 1957b, 1957c), which may be distinguished chemically by their amino acid compositions. These proteins, designated Tropomyosin-A (invertebrate) and Tropomyosin-B (vertebrate = Bailey's rabbit tropomyosin) by Kominz *et al.*, may be basic units used in the formation of myosin, a contractile protein of muscle fibrils (Bailey, 1948; Kominz *et al.*, 1954, 1957b; Yoshimura, 1955; Laki, 1957a).

However, the situation may be much more complicated since the distinction between types A and B was only made on the basis of major differences in amino acid composition, involving primarily glutamic acid, lysine, arginine, and amide residues in the tropomyosin molecule. Some differences of a lesser nature involving other amino acids, e.g. tyrosine and methionine, appear to be class

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specific, and it has been suggested by Laki's group (Kominz *et al.*, 1957b) that differences specific to species might be found if a sufficiently thorough investigation were performed.

Undoubtedly, knowledge of the sequence in which the amino acid residues occur in the tropomyosin molecule would be of great value in helping to classify this protein, and make it possible to explain some of its physical, chemical, and biochemical properties or even its possible role in muscle contraction.

For this reason, an analytical study of cod tropomyosin was begun some years ago, with the intention to resolve the sequence of amino acids in its molecule. The choice of cod muscle as the starting material in this study was simply made because of this Station's general interest in cod muscle proteins.

This paper deals with the preparation of cod tropomyosin. with the proximate analysis of the protein and with the determination of its amino acid composition.

MATERIALS

Tropomyosin. Two preparations of tropomyosin were made, the first a purified product which was prepared in bulk (about 100 g), and the second a highly purified material[3] of which only 500 mg was obtained. The starting material for both preparations was fillets of fresh Atlantic cod (*Gadus callarias*).

The bulk preparation was made in batches of 10 to 15 g each following the alcohol precipitation procedure of Dingle and Odense (1959), which was slightly modified to adapt it to the handling of a larger quantity of fillets per batch (about 4000 g). These modifications included: the use of a filter press rather than a centrifuge in the first solvent-treatment stages, the use of a continuous Webcel dialyser for all dialyses, and final precipitation of the tropomyosin with acetic acid followed by washing with alcohol and ether.

A preliminary check on the purity of each batch was the determination of tryptophan. When there was less than 0.04% (dry basis), the preparation was subjected to further tests of purity by means of moving-boundary electrophoresis[4]. The batch was accepted for use whenever the purity of the protein was 95 to 100%. Acceptable preparations were combined and thoroughly mixed; the mixture, "bulk tropomyosin", was used in the studies reported below. The electrophoretic pattern of a representative batch is given in Fig. 1.

The descending side of the pattern showed the presence of one protein component other than tropomyosin whereas the ascending side indicated that a second impurity was present. Planimetry showed that tropomyosin constituted 96% of the total protein and the impurities 4%. One of these impurities was probably actin. It was assumed that the amino acid compositions of the two impurities would be sufficiently similar to permit calculations on the basis of actin only. This appeared justifiable because the correction for total impurities is small.

[3]Prepared by Dr P. H. Odense of this Station.
[4]Carried out by Dr J. R. Dingle of this Station, using Spinco Model H apparatus.

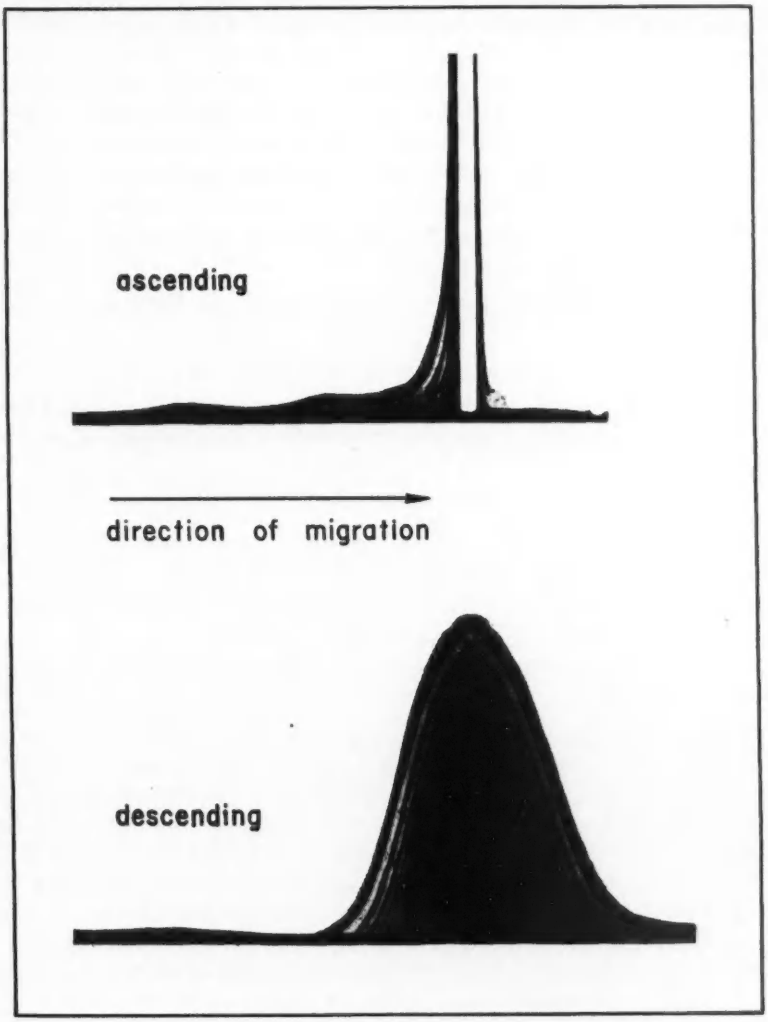

FIG. 1. Electrophoretic pattern of cod tropomyosin (bulk preparation).
Solvent: 0.10*M* KCl + K phosphate, $\Gamma/2 = 0.15$, pH 7.
Temperature: 1.2°C.
Duration of electrophoresis: 309 min.
Field strength: 4.4 volts/cm; current: 30 milliamperes.
Concentration: 0.862 mg N/ml.
Migration from left to right.

Highly purified tropomyosin was prepared following Bailey's (1948) procedure. Three consecutive steps of purification by precipitation with ammonium sulphate were employed; the final protein was precipitated with ammonium sulphate concentrations between 1.83 and 2.84 molar (45 and 70% saturation at 20°C). This product was electrophoretically homogeneous; the purity of the protein was probably better than 99%.

Resins and *chemicals* for use with the Beckman/Spinco Amino Acid Analyzer were of the quality specified in the Instruction Manual (Spackman, 1960).

Carboxypeptidase. Proteinase-free preparation as obtained from Nutritional Biochemicals, Inc., Cleveland, Ohio.

Zeokarb 225. Obtained as Permutit Q from the Permutit Company, New York.

METHODS

Moisture. The weight lost by preparations kept at 105°C for 24 hr, followed by 1 hr at room temperature in a vacuum desiccator with phosphorus pentoxide as the drying agent.

Ash. Residue at 525°C; method 29.13 A.O.A.C. (1955).

Nitrogen. Micro-Kjeldahl; selenium catalyst.

Tryptophan. Spies and Chambers (1949).

Sulphur. Oxidation in Parr bomb with sodium peroxide, followed by gravimetric determination of sulphate as barium sulphate.

Cystine + cysteine. Block and Bolling's (1951) adaptation of the Winterstein–Folin reaction.

Nucleic acid. From difference in absorbance at 261 mμ of solutions of tropomyosin before and after treatment with perchloric acid. Calculation following Dingle and Odense (1959). Results are expressed as nucleic acid, although the compounds present in the tropomyosin preparations may have been smaller (non-dialysable) polynucleotides or polynucleosides.

N-terminal amino acids. Sanger's fluorodinitrobenzene procedure (see Fraenkel-Conrat *et al.*, 1955) followed by paper chromatography.

C-terminal amino acids. Digestion with carboxypeptidase; isolation of liberated amino acids with Zeokarb 225 and identification of these acids by paper chromatography (see Fraenkel-Conrat *et al.*, 1955).

Amino acids. Ion-exchange chromatography of acid hydrolysates of tropomyosin following Spackman *et al.* (1958) using the Beckman/Spinco Automatic Amino Acid Analyzer.

Hydrolysis. Samples, approximately 250 mg each, were refluxed with 5 ml constant boiling hydrochloric acid for 22 hr. Acid was removed by distillation under reduced pressure (repeated three times after addition of water). The practically acid-free residue was taken up in citrate buffer pH 2.2 ("sample-diluent" buffer containing thiodiglycol, BRIJ and octanoic acid; see Spackman,

1960) and made to the volume required to obtain a nitrogen concentration of approximately 0.150 mg/ml. Two millilitres of this solution was used on each column.

Corrections for hydrolytic losses. Determined by analysis of 6-, 12-, 22-, 40-, and 72-hr hydrolysates of tropomyosin. The factors applied to results of 22-hr hydrolysates were: threonine 1.10; serine 1.06; valine 1.03; and isoleucine 1.03. Other amino acids needed no correction.

RESULTS

Proximate Analysis

The mean values of at least three determinations of each constituent are given in Table I.

Table I. Proximate analysis of bulk preparation of cod tropomyosin.

Constituent	Content	Constituent	Content
	%		%
Moisture	2.93	Nitrogen	15.44
Ash	3.49	Sulphur	0.728
Nucleic acid	1.50	Cysteine+	
Actin	3.7*	cystine	0.575
Tropomyosin	88.4*	Tryptophan	0.032

*Total protein by difference; the ratio actin: tropomyosin = 4 : 96 determined by planimetry of electrophoretic pattern.

Terminal Amino Acids

With Sanger's fluorodinitrobenzene method, no N-terminal amino acids were found. The C-terminal acid, liberated by treatment with carboxypeptidase, was isoleucine. The rates at which different amino acids were released from tropomyosin (Table II) were used to estimate their sequence in the molecule; the first three occurred in the order: -thr-ser-ileu.

Table II. Release of amino acids from cod tropomyosin preparation upon treatment with carboxypeptidase.

Duration of enzyme treatment	Intensities of amino acid zones on paper chromatograms[§]						
	Ileu	Ser	Thr	Asp	Ala	Gly	Glu
minutes							
0	0	0	0	0	0	0	0
15	**20**	10	5	1	1	0	2
30	30	**30**	10	3	2	1	4
60	**40**	30	**20**	10	5	3	6
120	80	30	20	**20**	15	10	8
240	100	30	20	20	**20**	10	8

[§]The technique used did not permit the detection of methionine. The intensities and times at which the several amino acid zones attained maximum values are indicated in bold type.

Amino Acid Content

Three hydrolysates of cod tropomyosin were analysed by the Spackman *et al.* (1958) method; several replicates were run on each hydrolysate, so that at least seven, usually ten, and sometimes fifteen values were obtained for each amino acid. The nitrogen contents of the hydrolysates were used to express the results in terms of millimoles amino acid per 17.46 g of nitrogen, the latter being the amount of nitrogen equivalent with 100 g of pure tropomyosin in the bulk preparation (calculated from Table I). This total nitrogen content was composed of nucleic acid-N 0.27 g, actin-N 0.69 g, tropomyosin-N 16.50 g (assuming identical nitrogen contents for actin and tropomyosin and 16.0% for nucleic acid). The mean amino acid contents, their standard errors, and the number of observations from which they were obtained are listed in Table III.

Table III. Amino acid content of bulk preparation of cod tropomyosin.

Amino acid	Number of analyses	Amount per 17.46 g N		Std. error Mean
		Mean	Std. error	
		millimoles	*millimoles*	%
Lysine	15	119.6	0.78	0.65
Histidine	15	6.98	0.07	1.00
Ammonia	15	66.9	1.34	2.00
Arginine	14	43.7	0.44	1.01
Aspartic acid	10	110.0	1.48	1.35
Threonine*	10	30.9	0.47	1.53
Serine*	10	36.6	0.41	1.13
Glutamic acid	10	212.5	1.98	0.93
Proline	7	3.14	0.10	3.18
Glycine	10	20.4	0.26	1.27
Alanine	10	105.1	1.27	1.21
Cystine/2	–	5.41†	–	–
Valine*	10	28.3	0.42	1.49
Methionine	10	20.3	0.23	1.13
Isoleucine*	10	31.8	0.31	0.97
Leucine	10	102.4	0.86	0.84
Tyrosine	10	16.7	0.19	1.14
Phenylalanine	10	4.89	0.12	2.45

*Corrected for hydrolytic losses.
†From S content less methionine-S (5.40) and from direct cystine determination (5.41).

DISCUSSION

The nitrogen content of pure cod tropomyosin, calculated from the nitrogen distribution in the bulk preparation, was 16.50%. This is slightly lower than the value of 16.7% usually accepted for other vertebrate tropomyosins (e.g. Bailey, 1948; Kominz *et al.*, 1954). However, direct determination of the nitrogen content of the highly purified cod tropomyosin preparation never yielded results

higher than 16.5%. The latter value has therefore been used in this paper as the actual value for cod tropomyosin.

The precision of all the amino acid values listed in Table III appears quite acceptable. Even the proline content, which is the least precise of the data because its value is low and the method is relatively insensitive for this amino acid, has a small standard error. To obtain the amino acid composition of pure cod tropomyosin from the data of Table III, a correction must be applied to the value for each acid for the amount of that acid contributed by the actin impurity of the bulk preparation. These corrections were determined by carefully analysing a preparation of highly purified cod actin[3]; the mean values of two determinations (unpublished results very similar to those of Kominz *et al.*, 1954) were used. The results are given in Table IV.

TABLE IV. Amino acid composition of cod tropomyosin.

Amino acid	Amount in bulk preparation (17.46 g N)	Amount in actin (0.69 g N)	Pure cod tropomyosin (16.50 g N)	Recovery of nitrogen in cod tropomyosin	
	millimoles	*millimoles*	*millimoles*	*grams*	%
Lysine	119.6	1.9	117.7	3.30	20.0
Histidine	6.98	0.72	6.26	0.26	1.6
Ammonia	66.9	4.5	62.4	0.87	5.3
Arginine	43.7	1.6	42.1	2.36	14.3
Aspartic acid	110.0	3.2	106.8	1.50	9.1
Threonine	30.9	2.4	28.5	0.40	2.4
Serine	36.6	2.0	34.6	0.48	2.9
Glutamic acid	212.5	4.0	208.5	2.92	17.7
Proline	3.14	1.69	1.45*	0.02	0.1
Glycine	20.4	3.0	17.4	0.24	1.5
Alanine	105.1	2.8	102.3	1.43	8.7
Cystine/2	5.41	0.20	5.21	0.07	0.4
Valine	28.3	1.9	26.4	0.37	2.2
Methionine	20.3	1.3	19.0	0.27	1.6
Isoleucine	31.8	2.4	29.4	0.41	2.5
Leucine	102.4	2.6	99.8	1.40	8.5
Tyrosine	16.7	1.4	15.3	0.21	1.3
Phenylalanine	4.89	1.06	3.83	0.05	0.3
			Totals	16.56	100.4

*Proline by direct determination on highly purified tropomyosin: 1.88.

As may be seen, the corrections were usually small compared with the uncorrected values. This was not so for proline. To check the result for that amino acid, direct determinations were made on the highly purified preparation of cod tropomyosin; the value obtained was 1.88 millimoles per 16.50 g of nitrogen, considerably higher than the value of Table IV, and probably more accurate.

A comparison of the amino acid content found for cod tropomyosin with the values reported elsewhere for various other tropomyosins (Table V) shows

TABLE V. Amino acid compositions, in moles/10^5 g of protein, of tropomyosins from different animals. (See the original publications referred to in this Table for the specific muscle from which the tropomyosins were isolated.)

Amnio acid	Cod	Rabbit	Cow	Frog	Carp	Haddock	Lamprey	Lobster	Squid[6]	Squid[7]	Clam[8]	Earthworm	Clam[8]	*Pinna nobilis*
	Type of tropomyosin													
	B	B	B	B	B	B	B	B	B	B	B	A	A	A
	References													
		Kominz *et al.*, 1957c	Kominz *et al.*, 1957c	Saad *et al.*, 1959	Saad *et al.*, 1959	Kubo, 1957	Saad *et al.*, 1959	Kominz *et al.*, 1957b	Kominz *et al.*, 1957b	Yoshimura, 1955	Kominz *et al.*, 1957b	Kominz *et al.*, 1957b	Kominz *et al.*, 1957b	Bailey, 1957
Lys	117.7	107	104	112.3	113.0	114	115.7	78	78	83	78	56	59	64.5
His	6.26	5.5	5.3	6.8	6.0	6	6.7	3	3	12	3.3	10	4	4.5
Amm	62.4	64	62	55.2	62.2	61	59.2	90	85	87	84	98	110	116
Arg	42.1	41	41	42.2	41.0	38	41.6	63	63	63	67	86	81	79
Asp	106.8	89	88	91.1	95.7	85	92.5	101	103	92	110	97	114	111
Thr	28.5	26	25	25.4	24.1	34	29.8	27	38	30	35	40	36	22
Ser	34.6	40	41	34.0	33.4	40	39.7	43	45	51	43	51	39	49
Glu	208.5	212	213	201.0	200.8	237	204.5	200	195	196	205	169	169	173
Pro	1.88	1.7	. . .	2.9	2.9	0	2.9	3	4	0	1.7	1.7	1.5	0
Gly	17.4	12	9	14.4	17.8	12	14.8	14	17	26	20	25	15	12
Ala	102.3	108	107	106.0	106.5	101	105.3	90	93	88	101	86	108	102
Cys/2	5.21	6.5	. . .	5.9	5.0	6.5	5.8	. . .	. . .	5.5	. . .	. . .	. . .	2.5
Val	26.4	27	27	32.0	36.8	29	35.1	33	24	23	40	29	28	35.5
Met	19.0	16	16	24.6	23.3	18	17.2	22	12	16	8	1.5	11	15.5
Ileu	29.4	30	30	28.8	29.8	32	32.7	12	25	18	27	35	22	28
Leu	99.8	95	95	94.8	106.6	101	87.6	88	86	88	88	124	106	103
Tyr	15.3	15	15	17.7	18.5	21	18.9	12	10	7	20	10	18	14
Phe	3.83	3.3	3.7	4.3	5.7	3.5	4.0	11	12	7	6.3	12	6	8.5
Net charge pH 8	93.1	89	94	82.4	80.3	109	80.5	70	72	65	86	26	33	24

[6]*Loligo pealeii.*
[7]*Ommastrephes sloani pacifus* STEENSTRUP.

clearly the similarity between cod tropomyosin and other vertebrate tropomyosins. It is also evident, however, that there are many differences. The most striking among the latter is that in aspartic acid content. In this respect, cod tropomyosin appears to resemble invertebrate tropomyosin more than the vertebrate type. This difference could not be explained on the basis of lack in precision of some of the listed values, an explanation which might be used for smaller differences in some of the other amino acid contents. The possibility still remains that differences in purity of the various preparations might account for the dissimilarity of the aspartic acid values.

If the general similarity between cod tropomyosin and other vertebrate tropomyosins may be interpreted to indicate that the molecular weight of its monomer must be of the order of 53,000, as it was found to be for the rabbit muscle protein (Adair *et al.*, 1949; Tsao *et al.*, 1951; Tsao and Bailey, 1953), the number of amino acid residues and the molecular weight could be calculated from the amino acid composition. This has been done in Table VI.

TABLE VI. Amino acid residues per molecule of cod tropomyosin.

Amino acid	Minimal molecular weight from amino acid composition	Number of residues for MW = app. 53,000	Molecular weight from number of residues
Lysine	850	62	52,700
Histidine	16,000	3	48,000
Amide	1,600	33	52,800
Arginine	2,400	22	52,800
Aspartic acid	940	56	52,600
Threonine	3,500	15	52,500
Serine	2,900	18	52,200
Glutamic acid	480	110	52,800
Proline	53,200	1	53,200
Glycine	5,700	9	51,300
Alanine	980	54	52,900
Cystine/2	19,200	3	57,600
Valine	3,800	14	53,200
Methionine	5,300	10	53,000
Isoleucine	3,400	15	51,000
Leucine	1,000	53	53,000
Tyrosine	6,500	8	52,000
Phenylalanine	26,100	2	52,200
	Total:	488	Mean: 52,540
	Less amide:	33	
	Residues per molecule:	455	

In earlier investigations, tropomyosin was considered not to contain proline. More recently, however, positive proline contents have been found (see Table V). It is evident from the results of this study that proline is definitely a constituent of cod tropomyosin and that there is probably one residue per molecule of the protein.

[9] *Loligo pealeii.*
[10] *Ommastrephes sloani pacifus* STEENSTRUP.

The occurrence of three residues of half-cystine (cystine/2) is of interest. This same number of residues was found by Saad *et al.* (1959) for carp tropomyosin but one less was reported by Kominz *et al.* (1954) for several other vertebrate tropomyosins. At least one of the half-cystine residues must be present in the cysteine form; the others may be present as two cysteines or as one cystine residue forming an –S–S– bridge in the molecule. The latter appears more likely when considering that oxidation of tropomyosin with performic acid prior to digestion with trypsin eliminated the initial lag-phase which was found when the digestion was carried out without previous oxidation (to be published). The presence of one –S–S– cross-linkage in the tropomyosin molecule is in agreement with the findings of Szent-Györgyi *et al.* (1959) for tropomyosin from rabbit muscle.

The absence of a free N-terminal residue and the occurrence of isoleucine in the C-terminal position agrees with findings for other tropomyosins (Bailey, 1951; Locker, 1954; Saad *et al.*, 1959). The C-terminal sequence in cod tropomyosin is exactly the same for the first three residues as that reported by Locker (1954) for rabbit tropomyosin. Beyond the third residue, the digestion results (see Table II) appear to indicate some differences. The most likely sequence based on the results of Table II is: -glu-gly-ala-asp-ileu-thr-ser-ileu. However, the reliability of this result decreases with increasing distance from the C-terminal residue, and judgement must be reserved until more accurate results become available.

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Observations on the Ecology of the Pacific Cod (*Gadus macrocephalus*) in Canadian Waters[1,2]

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ABSTRACT

In Canadian waters, Pacific cod are close to the southern limit of their range and appear to inhabit depths where temperatures are between 6° and 9°C. Seasonal variations in depth distribution are not as pronounced as those in the northwestern Pacific where there are much greater variations in the seasonal cycle of temperature.

Relatively high temperature experience in Canadian waters appears to be responsible for a more rapid initial growth rate (instantaneous rate, $g = 1.99$ between ages I and II; 0.64 between ages II and III, decreasing to 0.19 between ages IV and V) and a much shorter life span than elsewhere. Estimates of L_∞, the asymptotic length, range from 72.8 cm to 77.4 cm, while estimates of K, the rate at which growth approaches L_∞, range from 0.56 to 0.71.

Maturity is reached at two to three years of age—several years earlier than in colder regions of the North Pacific—and estimates of instantaneous total mortality rate range from 1.27 to 1.77 for fish of commercial size. Although these are probably overestimates, it is nevertheless apparent that total mortality rate is very high and that a large share is due to natural causes. Instantaneous natural mortality rate possibly exceeds 0.9.

INTRODUCTION

Not without good reason one is usually inclined to associate the word *cod* with the North Atlantic Ocean, for most of the world catch of gadoid fishes and particularly of representatives of the genus *Gadus* originates from that region. Less well known is the fact that cod of the genus *Gadus* contribute also to the fisheries production of the North Pacific Ocean, though admittedly in much smaller measure. The Pacific cod (*Gadus macrocephalus*), or grey cod as it is called by Canadian fishermen, is widely distributed, but its potential importance, at least along the shores of North America, is still a matter for conjecture. In the past decade the cod has risen to considerable prominence in the trawl fishery off the Canadian coast and consequently has created a need for knowledge of its ecology and population dynamics.

Extensive published data exist on the biology and ecological relationships of cod in waters of the northwestern Pacific, but only fragmentary information is available for the northeastern region.

This paper summarizes results of recent studies conducted by the Fisheries Research Board on the ecology of the cod in Canadian waters. Preliminary

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[2]Parts of this paper were presented at a Symposium on Fisheries Oceanography held at San Diego, California in June, 1959. Other contributions to the symposium are to be published in a report of the California Co-operative Oceanic Fishery Investigations.

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and approximate though some of the observations may be, an attempt has been made to draw comparisons with results of USSR investigations in the north-western Pacific, a region which is ecologically quite different from the north-eastern Pacific.

Along the Canadian coast, the Pacific cod is close to the southern limit of its range. Data to be presented suggest that in this region environmental stress, imposed either directly or indirectly by relatively high water temperature, is manifest in a high initial growth rate, early sexual maturity and a short life span.

NOMENCLATURE AND DISTRIBUTION OF THE PACIFIC COD

In North American literature the Pacific (grey) cod is recognized as *Gadus macrocephalus* Tilesius. It is similar in many respects to the famous Atlantic cod, *G. morhua* L., but on the basis of certain anatomical features (shape of the air bladder horns, colour of peritoneum and fins, etc.) Schultz and Welander (1935: 130) concluded that it bears closer resemblance to the Greenland cod, *G. ogac* Richardson. Some research workers in the USSR (but not all—cf. Rass, 1959: 244) regard these three species as subspecies of *G. morhua*, whence the Pacific cod becomes *G. morhua macrocephalus* (Svetovidov, 1948: 179; Moiseev, 1960: 558). In any event it is generally accepted that there is but one representative of the genus *Gadus* in the North Pacific Ocean and adjoining seas, and in this paper it will be referred to as *G. macrocephalus*, even though it may be deserving of only sub-specific rank.

Gadus macrocephalus is widely distributed around the great arc of the North Pacific Ocean (Fig. 1). Along the shores of eastern Asia, the southern limit of its range (not shown in the figure) is reported to be in the Yellow Sea along the west coast of Korea. Progressing northward, the Pacific cod is found along the eastern and western shores of the Sea of Japan, around the shores of Hokkaido and Sakhalin and along the Kurile Island chain. It occurs in the Sea of Okhotsk, along the east coast of Kamchatka and in the western Bering Sea as far north as the Gulf of Lavrentsia (Svetovidov, 1948: 180).

Along the coast of western North America, the northern limit of the cod's range is reported to be in the latitude of St. Lawrence Island (and around that Island, according to Cobb, 1927: 388). It occurs in the southeastern Bering Sea and apparently also along the Aleutian Island chain. To eastward, the cod is found along the Pacific side of the Alaska Peninsula, around the shores of the Gulf of Alaska and from there southward to the California coast of the United States.

The region between Cape Flattery and Destruction Island on the Washington coast (48°21′ N to 47°40′ N Lat.) may be regarded as the southern limit of fishing specifically for cod. Southward from Destruction Island, catches of cod are usually incidental to those of other species, and cease to be recorded in fishery statistics for waters south of Cape Blanco, Oregon (42°50′ N Lat.). Occasionally,

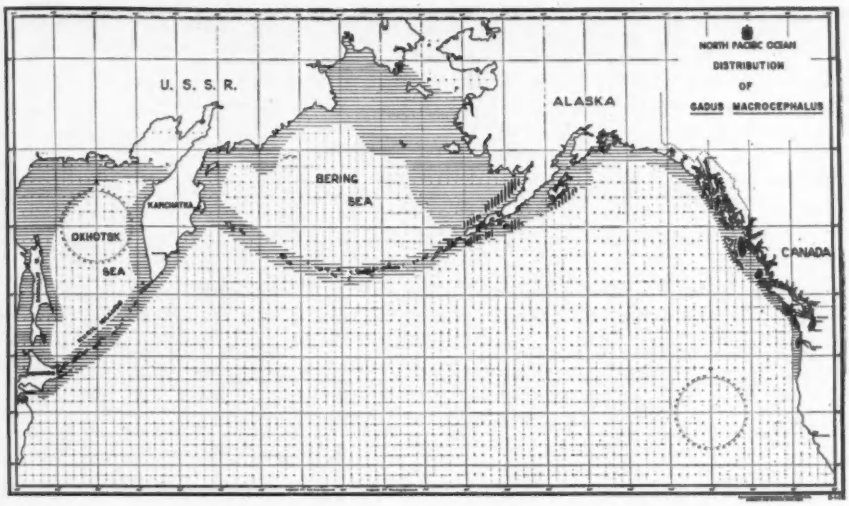

FIG. 1. General distribution of *Gadus macrocephalus* in the North Pacific Ocean and adjoining seas, adapted from Svetovidov (1948). Vertical shading depicts approximate location of the former fishery by North American nationals near the Alaska Peninsula, while solid areas refer to the present day fishery off Canada and the northwestern United States.

individual specimens are reported from California waters as far south as Pt. Piedras Blancas (35°33′ N Lat.—see Phillips, 1950: 439; 1951: 351; 1953: 559; 1958: 349).

PRODUCTION OF PACIFIC COD

1. General

The reported production of Pacific cod in 1957, according to fishery statistics published by the Food and Agriculture Organization of the United Nations, was 94,500 metric tons (about 200 million pounds) or less than one-twentieth of the cod production from the North Atlantic Ocean and adjoining seas. Of this catch, 69.5% was accounted for by Japan, 19.5% by the USSR, 5.7% by the USA, 3.2% by Canada and 2.1% by South Korea (no information was available on production by North Korea).

2. North American Waters

The fishery by North Americans for Pacific cod has a long and varied history, beginning in the early 1860's with landings at San Francisco from the Sea of Okhotsk (Cobb, 1927: 404). This long-distance operation continued in prominence until 1884, after which time grounds closer to home, principally those in the southeastern Bering Sea and along the southern shores of the Alaska Peninsula, assumed a dominant role. This latter fishery, pursued with hook and line, reached a peak production of 3,893,000 fish or roughly 44,000,000 lb (round

TABLE I. Production of Pacific cod from waters adjacent to Canada and the States of Washington and Oregon, in millions of pounds estimated round weight. Sources: British Columbia catch statistics, Department of Fisheries, Canada; records of the Fisheries Research Board of Canada; Fishery Statistics compiled by the Pacific Marine Fisheries Commission.

Year	Canada	Washington	Oregon	Total
1935	2.24	0.05	—	2.29
36	1.08	0.26	*	1.34
37	1.92	0.53	0.01	2.46
38	2.50	0.46	—	2.96
39	2.23	0.66	—	2.89
1940	2.23	0.65	—	2.88
41	1.29	1.57	*	2.86
42	0.90	1.18	0.03	2.11
43	2.12	1.03	0.03	3.18
44	1.26	1.04	0.03	2.33
1945	1.60	4.08	0.07	5.75
46	2.86	4.36	0.25	7.47
47	0.94	2.45	0.03	3.42
48	0.92	5.38	0.03	6.33
49	1.68	5.50	*	7.18
1950	2.47	6.35	0.04	8.86
51	5.72	8.42	0.12	14.26
52	4.89	10.00	0.12	15.01
53	3.45	8.20	0.18	11.83
54	5.70	15.41	0.78	21.89
1955	4.62	12.61	0.32	17.65
56	5.15	9.57	0.18	14.90
57	8.50	11.32	0.69	20.51
58	10.02	12.29	0.30	22.61
59	9.19	12.91	0.30	22.40

*Less than 5000 lbs.

weight) in 1916[3]. However, mainly because of economic problems, it declined to a relatively low level by 1933, where it remained until the late 1940's before proceeding to virtual extinction in the past decade.

The only other area along the North American coast where Pacific cod have been the object of extensive fishing is that adjacent to Canada and the State of Washington. In contrast to the history of events in western Alaska, this southern fishery is of relatively recent origin and is still in process of development.

Rapid development of an otter-trawl fishery for many species of groundfish along the exposed coast of British Columbia resulted in a substantial increase in cod production in the years following World War II (Table I). Between 1945

[3]These figures apply to the catch secured by the shore and vessel fisheries and transported to ports in Washington and California. Cod used for local consumption in Alaska are not included. Conversion to round weight is based on Cobb's data (1927: 444) for the years 1922 to 1925.

and 1950 the annual catch by Canadian and United States trawlers averaged about 6,500,000 lb, after which time it rose to new heights, principally in response to the demand for "fish sticks". Since 1951 the catch has varied between 12,000,000 and 23,000,000 lb per year with an average of 18,000,0000 lb for the years 1951 to 1959.

DISTRIBUTION OF COD IN WATERS ADJACENT TO CANADA

1. Areas of Concentration

While the Pacific cod occurs throughout Canadian coastal waters generally, it forms concentrations in well-defined areas and at particular times of the year. Fisheries involving Canadian and United States trawlers take place on these concentrations and are confined to relatively small segments of the continental shelf (Fig. 2). The most productive fishing areas lie in northern Hecate Strait including four main fishing grounds: "White Rocks" or Banks Island; the Warrior-Butterworth "edge" which is confluent with the "Two Peaks" ground at the northern end of the Strait and the Horseshoe-Cumshewa grounds in the lower central area. Farther to the south, in Queen Charlotte Sound, Pacific cod are taken principally along the southeastern edge of Goose Island Bank and along the northern edge of Cape Scott Bank. Off the lower west coast of Vancouver Island, cod are encountered on a number of restricted grounds (known locally as the "Firing Range", "Cabbage Patch" and "Forty-mile" or Big Bank) within the general confines of La Pérouse Bank, and also on or near Swiftsure Bank at the entrance to Juan de Fuca Strait. Still farther to the south, off the coast of the United States, concentrations are found mainly between Cape Flattery and Destruction Island, Washington. Minor quantities are encountered off the estuary of the Columbia River and the coast of Oregon. In addition to the offshore fishing areas, there are numerous small fishing grounds for cod within Canadian and United States territorial waters of the Strait of Georgia and Puget Sound.

2. Seasonal Bathymetric Distribution

Information on seasonal changes in the depths occupied by Pacific cod on banks adjacent to British Columbia has been obtained through a system of interviewing Canadian trawler captains. At time of landing, a report is obtained on the area of catch, hours of fishing, the catch of each species and the depths at which they were caught. While the reported depth of fishing is usually indicated by a range of depths, for particular fishing grounds it is usually narrow enough to permit calculation of a meaningful average depth. Reports of various fishermen are combined (with due weight given to size of catch) in order to obtain an average picture for each month and area. The data, as presented here, have been further consolidated to provide an average of conditions observed during the period 1954–58, inclusive. Throughout, only those individual landing records have been used in which at least 25% of the fare consisted of cod. This

arbitrary selection reduces, but does not entirely eliminate, the effect of concurrent fishing for species other than cod.

For none of the fishing grounds is it possible to trace the bathymetric cycle throughout the year, strictly from observation of the Canadian fishery. Fishing on offshore banks is limited seasonally by weather and also by seasonal variations in the availability of cod. It is possible, nevertheless, to infer, from trends in depth distribution evident during seasons of active exploitation, what the probable course of events is at other times of the year. Support for these inferences is to be found in information on the fishing pattern of the United States fleet, which is able to operate in exposed waters more or less on a year-round basis.

In general, the seasonal pattern of fishing suggests that cod inhabiting waters along the Canadian coast engage in a seasonal bathymetric cycle of migration. Greatest depths are reached in the winter months. Following spawning (January to March, depending on area) a migration takes place towards shallower regions of the coastal banks and this continues until late spring or early summer. The return movement to deeper water begins in mid-summer and continues until November or December. The vertical range of depths occupied during the year varies from area to area, but, as will be shown later, it is considerably less than that observed in most regions adjacent to the coast of Asia.

(a) Hecate Strait

During the months of November through February, Canadian trawlers are attracted to the White Rocks (Banks Island) ground which appears to be the principal spawning area for cod in Hecate Strait. At that time of year they are taken mainly between depths of 55 to 65 fathoms (100–120 m). Spawning apparently reaches a peak during the month of February, after which catch per unit of effort begins to decline. Coincident with this decline a fishery for cod begins to develop 30 to 60 miles to the northward along the Butterworth-Warrior edge and on the Two Peaks ground. Fishing in this region usually reaches its maximum in April, at which time the average depth inhabited by the cod is approximately 40 fathoms (about 75 m).

A northward migration from the White Rocks ground to shallow grounds in the northern part of the Strait is suggested by this northward movement of the fishery, but remains to be substantiated by tagging[4]. If true, it would accord with observations on the seasonal migrations of the lemon sole or English sole (*Parophrys vetulus*) in the same general area (cf. Ketchen, 1956: 659).

Usually from late April through early June, cod are encountered at depths of 30 to 35 fathoms (55–65 m) and in some years may be found right on the

[4]At time of writing it is too early to comment fully on the results of tagging conducted during February, 1960, on the White Rocks grounds. Initial recaptures were mainly from the area of tagging with 17 from the Two Peaks ground (60 miles to the north of the tagging site). However, there were also 4 returns from the Horseshoe ground (45 miles south of the tagging site).

edge of the bank as shallow as 17 to 20 fathoms (31–37 m). In northern Hecate Strait, the cod fishery usually comes to an end in late spring, because the cod either cease to remain in sufficient concentration to attract fishing or move into areas which cannot be touched with trawl nets.

About 80 miles to the south of the Butterworth-Warrior "edge", namely, on the Horseshoe ground, a fishery for cod usually develops in late spring and, as on the northern grounds, it occurs in relatively shallow water between 26 and 40 fathoms (48–73 m). These fish may be emigrants from the winter spawning area at White Rocks or they may belong to a separate population having its wintering ground in southern Hecate Strait.

From June onwards cod become increasingly scarce on all fishing grounds in Hecate Strait. Available records suggest that the months of May to June mark the period of maximum advance towards shallow water and that thereafter they move gradually towards deep water where they once again become available to the fishery (usually in November).

The foregoing remarks are best summarized by the data in Table II which provides a composite picture (weighted to the relative size of the catch on the various grounds) of the bathymetric distribution of cod in Hecate Strait. As a rule, greatest depth are reached in November (average 66 fathoms or 120 m) and shallowest depths in May or June (34–35 fathoms or 62–64 m).

TABLE II. Monthly average depth distribution of cod in Hecate Strait as based on observations for years 1954–55 to 1957–58, inclusive. (1 fathom = 1.83 m).
In this and succeeding tables, data based on fewer than 10 observations are in brackets.

Month	Number of observations	Depth (*fathoms*) Av.	Range	Month	Number of observations	Depth (*fathoms*) Av.	Range
Oct.	(2)	(38)	(30–41)	Apr.	71	14	39–42
Nov.	17	66	52–75	May	64	34	22–41
Dec.	19	58	54–64	June	22	35	18–47
Jan.	42	55	48–69	July	15	43	41–45
Feb.	45	56	53–65	Aug.	(2)	(44)	(42–45)
Mar.	119	49	45–55	Sept.	(2)	(53)	(52–54)

(b) QUEEN CHARLOTTE SOUND

The principal fishing grounds for cod in this area lie along the southeastern edge of Goose Island Bank and the northern edge of Cape Scott Bank. Insofar as the Canadian fleet is concerned, the fishery occupies a fairly short period of each year, usually May to August. Thus, there exists only fragmentary information on the seasonal bathymetric cycle. As in Hecate Strait, there is a suggestion that shallowest depths are reached in the months of May and June: about 46 to 51 fathoms (84–93 m) on Cape Scott Bank; about 56 fathoms (102 m) on Goose Island Bank (see Tables III and IV). Thereafter a movement towards

TABLE III. Monthly average depth distribution of cod on Cape Scott Bank as based on observations for years 1954–55 to 1957–58 inclusive.

Month	Number of observations	Depth (*fathoms*) Av.	Range	Month	Number of observations	Depth (*fathoms*) Av.	Range
Oct.	(1)	(56)	(45–67)	Apr.	18	52	49–55
Nov.	(1)	(83)	(82–85)	May	36	46	43–52
Dec.	(2)	(35)	(30–52)	June	36	51	44–58
Jan.	(1)	(55)	—	July	26	62	55–71
Feb.	(0)	—	—	Aug.	26	63	59–67
Mar.	(9)	(44)	(43–45)	Sept.	(5)	(64)	(59–68)

TABLE IV. Monthly average distribution of cod on Goose Island Bank as based on observations for years 1954–55 to 1957–58 inclusive.

Month	Number of observations	Depth (*fathoms*) Av.	Range	Month	Number of observations	Depth (*fathoms*) Av.	Range
Oct.	(1)	(59)	—	Apr.	(5)	(58)	(55–61)
Nov.	0	—	—	May	19	57	57–58
Dec.	0	—	—	June	20	56	50–62
Jan.	0	—	—	July	21	61	60–63
Feb.	0	—	—	Aug.	(8)	(63)	—
Mar.	(1)	(72)	—	Sept.	(1)	(60)	—

deeper water is indicated, although there is a scarcity of reliable data for months beyond August.

These observations are in general accord with those of Alverson (1960), based on records of the United States trawl fishery for cod on the Cape Scott and Goose Island Banks. Alverson's data (1955–57 average) suggest that cod on the latter bank reached their shallowest depth, about 60 fathoms (110 m), between May and July and their greatest depth, about 75 fathoms (135 m), in mid-winter. On Cape Scott Bank, shallowest depths were reached between June and August (about 65 fathoms or 120 m) and greatest depths in early winter (about 78 fathoms or 143 m)[5].

In comparison with Hecate Strait, the cod of Queen Charlotte Sound appear to occupy greater depths throughout the year and the amplitude of the annual bathymetric cycle is less.

[5]While Canadian observations are in general accord with those of United States investigators in respect to the timing and direction of seasonal changes in depth distribution, the observed absolute depths are somewhat less. Probably this can be attributed to the fact that Canadian and United States trawling fleets in Queen Charlotte Sound fish with different emphasis on species of groundfish which occur more or less in association with Pacific cod. In general the Canadian fleet fishes for shallow-water species such as rock sole (*Lepidopsetta bilineata*) as well as cod, while the United States fleet operates with greater emphasis on deep-water fishes (such as *Sebastodes* spp.). This serves to emphasize the limitations of commercial catch records for making observations on a particular species when fishing interest is not restricted entirely to that species. Although an attempt has been made to select out the effects of fisheries for species other than cod it can be done with only partial success.

(c) Lower west coast of Vancouver Island

The most southerly of the important fishing areas for cod in Canadian waters are La Pérouse Bank and Swiftsure Bank. Because of the topography of the former, it is difficult for the fishing fleet to maintain contact with cod schools for any great length of time each year. The range of fishable depths on grounds frequented by cod is limited, and hence if they move away they cannot be followed as systematically as on the Cape Scott and Goose Island Banks. Thus the fishery is usually compressed to a very few months, and seasonal trends in depth are more difficult to detect.

On the so-called Firing Range (a small basin on the inshore side of La Pérouse Bank) cod are caught usually between depths of 35 and 43 fathoms (65–80 m) during the May-July period. At the same time of year the nearby "Cabbage Patch" yields its best catches and these originate from depths of 36 to 40 fathoms (66–73 m). On the southeast and southwest corners of La Pérouse, namely, on Forty-mile Bank (Big Bank), cod fishing comes into prominence in the late summer and fall, after production from inshore grounds has passed its peak. Here the depths of fishing range from 40 to 46 fathoms (73–84 m), somewhat deeper than on inshore banks.

Catches from the Swiftsure Bank area, at the entrance to Juan de Fuca Strait, are made principally in the May-July period and at depths of 24 to 28 fathoms (44–51 m).

Table V is a composite of observations on the various fishing grounds off the lower west coast of Vancouver Island. Cod appear to be most available to the Canadian fleet during the inshore or shallow-water phase of the annual bathymetric cycle. As in regions farther to the north, there appears to be a movement toward deeper water during the late summer and early fall. Again, these observations are in general agreement with those made by Alverson (1960) on the cod fishery by United States vessels on adjacent grounds, between Cape Flattery and Destruction Island. There, during 1955-57, shallowest depths appeared to be reached about July or August (35–45 fathoms or 76–78 m).

Table V. Monthly average depth distribution of cod on grounds off the lower west coast of Vancouver Island, as based on observations for years 1954–55 to 1957–58, inclusive.

Month	Number of observations	Depth (*fathoms*) Av.	Range	Month	Number of observations	Depth (*fathoms*) Av.	Range
Oct.	22	43	37–47	Apr.	35	35	24–52
Nov.	(8)	(43)	(40–48)	May	89	37	24–44
Dec.	0			June	73	35	24–46
Jan.	0			July	21	36	23–49
Feb.	0			Aug.	13	38	31–43
Mar.	(8)	(30)	(23–45)	Sept.	15	45	39–58

In the winter months the cod were usually encountered at depths between 60 and 65 fathoms (110–120 m).

SEASONAL MOVEMENTS IN RELATION TO THE PHYSICAL ENVIRONMENT

In the foregoing section, the seasonal bathymetric distribution of cod in waters adjacent to the Canadian coast was described in rather general terms. For particular years and areas it is possible to draw some approximate comparisons with observations of seasonal changes in the oceanography of the continental shelf—if only to gain a preliminary appreciation of the cod's environmental experience in this southern part of its range.

A series of synoptic oceanographic surveys in Hecate Strait and Queen Charlotte Sound was first undertaken by the Pacific Oceanographic Group between May 1954 and June 1955. Data from a few of the numerous stations occupied during these surveys have been selected for comparison with observations on the movements of cod. The positions, chosen for their proximity to known cod fishing grounds, are shown in Fig. 2, as Stations A, B and C, adjacent to the Two Peaks, White Rocks and Goose Island-Cape Scott grounds, respectively.

Synoptic surveys of the continental shelf were resumed in May of 1957, along the west coast of Vancouver Island and in the entrance to Queen Charlotte Sound. Oceanographic data for the years 1957 and 1958 are based on observations at Stations D and E, at the entrance to the Cape Scott-Goose Island gully and at the edge of La Pérouse Bank, respectively. In addition there are available, for these year, twice-daily bathythermograph observations from the lightship at Swiftsure Bank (Station F in Fig. 2). These observations together with those for the other stations mentioned are taken from the published data records of the Pacific Oceanographic Group.

The synoptic surveys of 1954–55 were made at 2-month intervals, while those of 1957–58 were made at 3- to 4-month intervals. Clearly, such infrequent monitoring cannot be expected to provide more than a broad description of the cod's physical environment. In the present study, primary consideration has been given to the relationship between temperature and the movement of cod. The main reason for this exclusive and undoubtedly oversimplified treatment is that it provides a convenient means of drawing comparisons with observations which have been made in the northwestern region of the Pacific. Nevertheless, there is a substantial weight of evidence in support of the view that temperature plays an important role in the general distribution, behaviour and metabolic processes of the cod. Hence, while acknowledging the possible influence of such factors as salinity, oxygen concentration, pH, etc. and the possibility that temperature may at times be of only indirect importance, we shall proceed to examine the relationship between the seaonal cycle of temperature and the seasonal bathymetric distribution of the cod, first in Canadian waters and then in the northwestern Pacific.

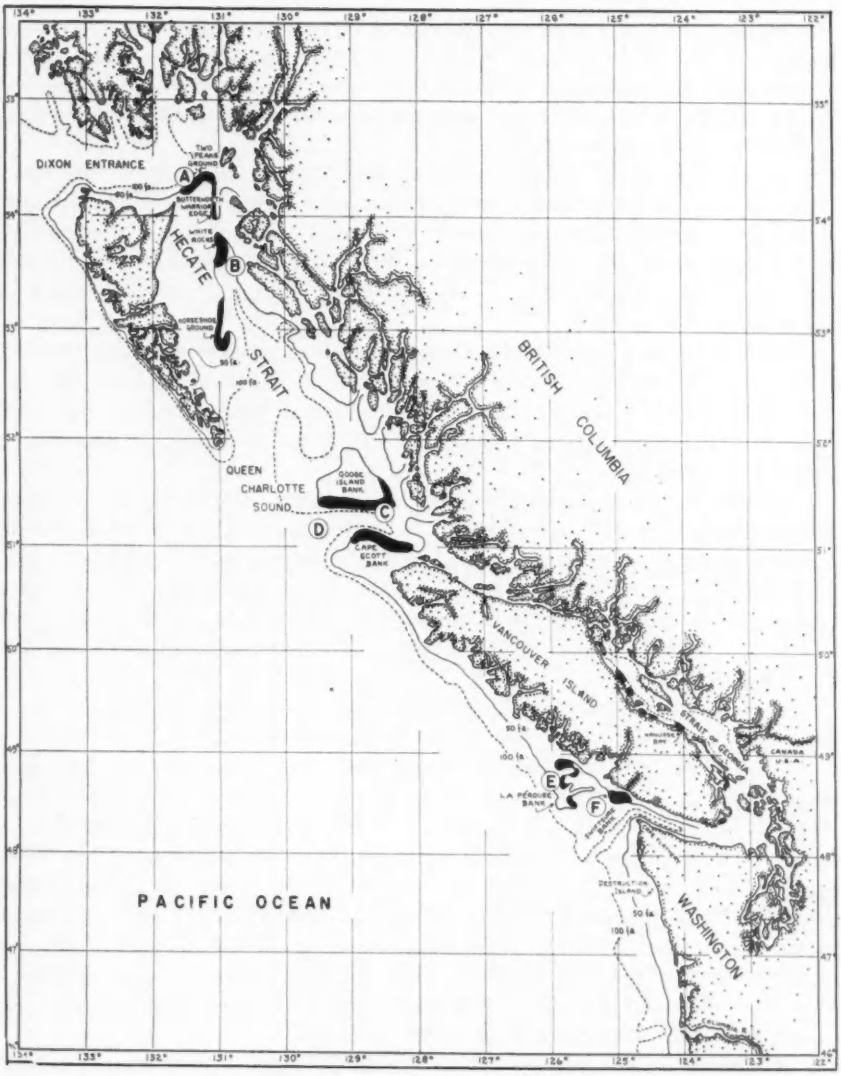

FIG. 2. Principal trawling grounds for Pacific cod on banks along the Canadian coast and positions of hydrographic Stations A–F referred to in the text.

1. Observations in Canadian Waters

(a) Hecate Strait and Queen Charlotte Sound

Figures 3, 4 and 5 show the seasonal variations in temperature structure at Stations A, B and C, respectively, as derived from the 1954–55 surveys of the northern British Columbia coast. Shown also are the average depths and ranges of depths over which cod were encountered in economic concentrations by the Canadian trawler fleet.[6]

On the Two Peaks ground at the extreme northern end of the Hecate Strait Bank, data on cod distribution are rather fragmentary, as the fishery occupies a very short period of the year (Station A, Fig. 3). These limited observations, in a region which is representative of the coldest conditions on the British Columbia coast, suggest that during 1954 and 1955 cod occupied water of approximately 6° to 7°C.

During this same period on the main fishing grounds on Hecate Strait, namely, between the Butterworth-Warrior "edge" and the Horseshoe ground (Station B, Fig. 4) a majority of the records suggests that cod remained within the range of 6° to 8°C throughout the period of observation. Virtually all were within the range of 6° to 9°C.

Farther to the south in Queen Charlotte Sound (Station C, Fig. 5) commercial catches of cod were obtained by Canadian trawlers at depths where water temperature was between 6° and 7°C. For the early months of 1955, information on depth distribution is available in data from the United States fishery. Average depths for the months of January through March, 1955, shown in Fig. 5 are from Alverson (1960: 56–57). Temperature at these depths was roughly 6° to 7°C.

Thus, it appears that cod in the northern part of the Canadian coast inhabited waters of 6° to 7°C, more or less throughout the year.

From May, 1957, onwards, oceanographic surveys of coastal and high seas regions have provided a certain amount of information on the seasonal cycle of temperature at Station D (see Fig. 2). This Station lies westward of Station C, in the entrance to the trench which separates the Goose Island and Cape Scott Banks. As shown in Fig. 6, the 1957 and 1958 distribution of Canadian cod catches (with the exception of those on the Cape Scott Bank in 1958) was largely within the range of 6° to 7°C. All were within the 6° to 9°C range. Figure 6 includes data from the United States fishery in October, November and December, 1957 (from Alverson, loc. cit.). In those months, cod appeared to be occupying depths where temperatures were between 7° and 8°C.

Reviewing the results for northern British Columbia waters, it appears that cod are to be found most commonly at depths where temperatures are between 6° and 7°C. Almost all of the commercial catches are made within the 6° to 9°C range.

[6]Because temperature is plotted on a time-depth scale, the impression is created in these figures that cod are caught in mid-water. Actually they are caught on or near the bottom.

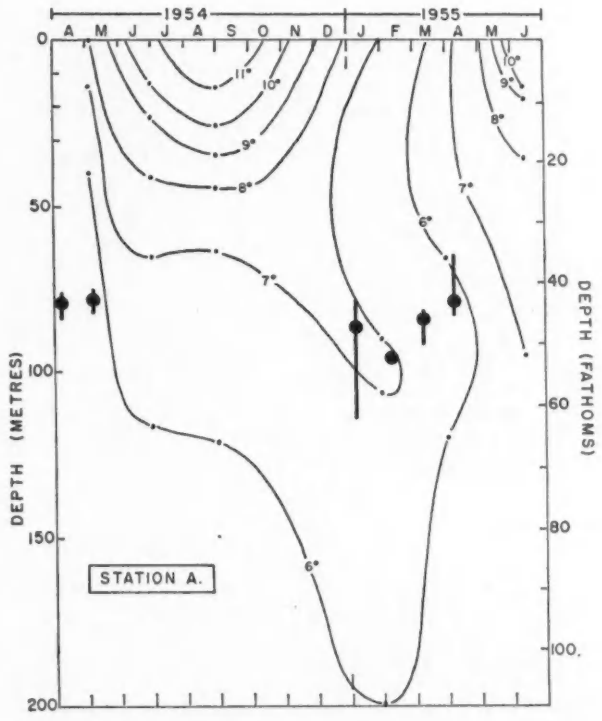

FIG. 3. The seasonal cycle of water temperature at Station A and its relation to the monthly depth distribution of Canadian commercial catches of cod from the Two Peaks ground in northern Hecate Strait during 1954–55.

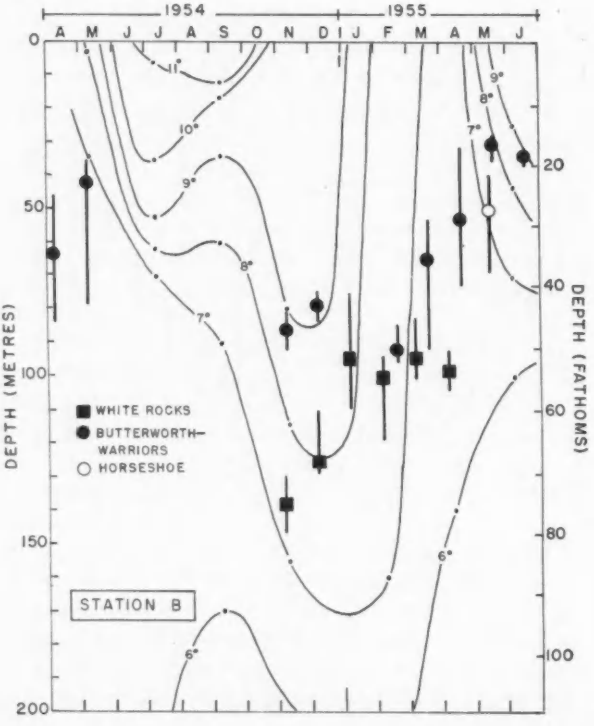

FIG. 4. The seasonal cycle of water temperature at Station B and its relation to the monthly depth distribution of Canadian commercial catches of cod from the Butterworth-Warrior, White Rocks and Horseshoe grounds of Hecate Strait during 1954–55.

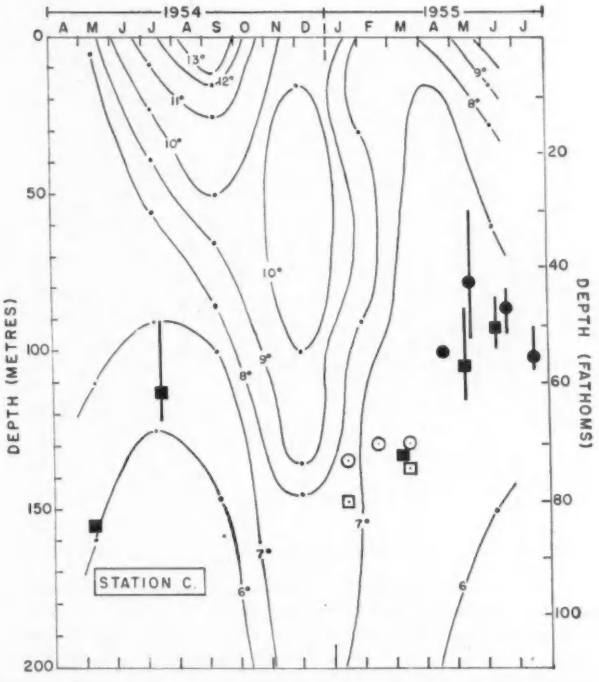

FIG. 5. The seasonal cycle of water temperature at Station C and its relation to the monthly depth distribution of Canadian commercial catches of cod on the Goose Island ground (solid squares) and Cape Scott ground (solid circles) in Queen Charlotte Sound during 1954–55. Data pertaining to the United States fishery in these areas during January–March, 1955, shown as open squares and open circles, respectively.

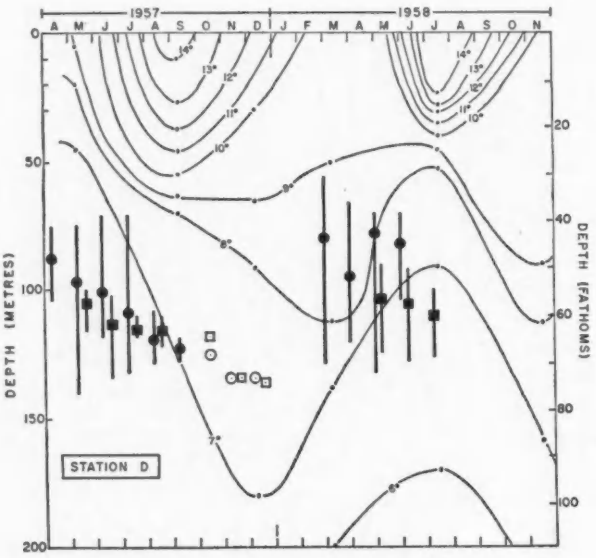

FIG. 6. The seasonal cycle of water temperature at Station D and its relation to the monthly depth distribution of Canadian commercial catches of cod on the Goose Island ground (solid squares) and Cape Scott ground (solid circles) in Queen Charlotte Sound during 1957–58. Data pertaining to the United States fishery in these areas during October–December, 1957, shown as open squares and open circles, respectively.

(b) Lower west coast of Vancouver Island

Synoptic oceanographic data for this southern region of the Canadian coast are based on observations at Station F (Fig. 2). These are presented in Fig. 7 with related information on cod distribution for the period 1957–58. Most of the latter data fall between the isotherms of 7° and 8°C, but in a few cases, it is suggested that catches were made at temperatures up to 10°C.

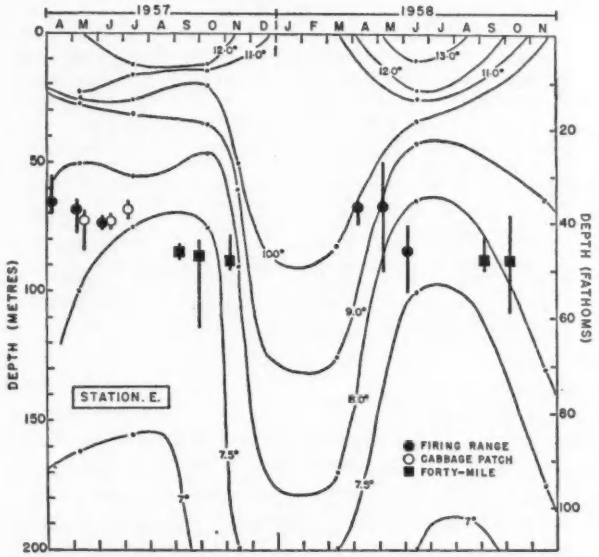

Fig. 7. The seasonal cycle of water temperature at Station E and its relation to the monthly depth distribution of Canadian commercial catches of cod on various grounds associated with La Pérouse Bank, off the lower west coast of Vancouver Island in 1957–58.

Average depths of fishing by United States trawlers during October, November and December, 1957, on the adjacent Cape Flattery-Destruction Island grounds were 51, 66 and 57 fathoms, respectively (data from Alverson, 1960: 56). Station E temperature for these months and depths were roughly within the range of 7.5° to 9.5°C.

These observations for the general area of La Pérouse Bank suggest that cod inhabit slightly warmer water than in regions farther to the north (Queen Charlotte Sound and Hecate Strait). Observations at Swiftsure Bank (Station F in Fig. 2) seem to confirm the observations at Station E that cod do indeed inhabit water which is warmer than 8°C. A Canadian fishery occurs along the inshore side of Swiftsure Bank (about 6 miles NE of the lightship, 48°33′N, 124°49′W), mainly during the months of May to July. Cod are taken at depths

ranging narrowly between 22 and 26 fathoms (40–48 m). Monthly averages of twice-daily temperature readings at depths of 25 to 27 fathoms (as determined from the lightship bathythermograph data) are given in Table VI. Shown also are the May-July catches of cod from the Swiftsure area. Unfortunately, records of the fishing operations were not sufficiently voluminous or detailed to permit a breakdown of catch by day for comparison with the daily temperature observations. However Table VI suggests that cod were caught at temperatures at least as high as 7.7°C and probably as high as 9.0°C.

TABLE VI. Summary of temperature observations at Swiftsure lightship and record of Canadian cod catch on the Swiftsure Bank.

Year	Month	Temperature at 25 fathoms		Canadian catch
		Monthly mean	Range	
		°C	°C	*lb*
1957	May	8.5	7.9–8.9	79,000
	June	8.5	8.0–9.2	52,000
	July	8.5	8.0–8.7	20,000
1958	May	8.5	7.7–9.4	53,000
	June	8.9	8.2–9.5	59,000
	July	8.3	7.7–8.8	—

(c) STRAIT OF GEORGIA

In passing, it is worthwhile to comment on observations of cod distribution in the inshore waters of the Canadian coast. The main fishing grounds are in the Strait of Georgia, in particular localities along the east coast of Vancouver Island. One is Nanoose Bay, which is fished only during the months of February and March when cod are congregated there for spawning, at depths of 40 to 50 fathoms (70–90 m). Temperatures at these depths in March of 1950 appeared to be within the range of 7.5° to 8.5°C (cf. Waldichuk, 1957: 348).

(d) SUMMARY

On the basis of observations in 1954–55 and 1957–58, it appears that the main concentrations of Pacific cod on banks adjacent to the Canadian coast are to be found between the isotherms of 6° and 9°C. In the northern sector of the coast, they tend to favour the lower part of this range (6°–7°C) and the upper part (7°–9°C) in the southern sector. In some instances, noted only in the latter region, there may be occasions when cod occur in water which is over 9°C.

Although data are incomplete, there is evidence of a seasonal cycle in the depth distribution of cod which is more or less synchronous with the seasonal cycle of temperature. Greatest depths are reached by the cod during the November-February period (50 to 80 fathoms, depending on the area) and shallowest depths are reached during late spring or early summer (17–40 fathoms). Similarly, it is noted that the isotherms of 6°, 7° and 8° are generally deepest during winter and shallowest during late spring and early summer.

In the light of existing information it is, of course, impossible to say whether there is a direct, causal connection between changes in bottom temperatures and the inshore–offshore movements of cod. Such features as salinity and dissolved oxygen have been examined, but these fail to reveal variations which are synchronous with the movements of cod. However, the evidence in favour of water temperature must remain circumstantial until results of more detailed and direct studies are available.

2. Observations in the Northwestern Pacific Ocean and Western Bering Sea

The Pacific cod has been under investigation for many years in waters adjacent to the Soviet Union, Japan and Korea. Results of numerous studies are conveniently summarized in a publication by Moiseev (1953).

Two opposing patterns of seasonal vertical migration are evident in the northwestern Pacific. In what Moiseev terms the north boreal region (from the northwestern reaches of Bering Sea to the latitude of the North Kurile Islands and Strait of Tartary) cod occur in deep water in the winter months and in shallow water during the spring and summer. Spawning occurs in late winter or early spring. In these respects the behaviour is rather similar to that observed in Canadian waters[7]. There is, however, a pronounced difference in the amplitude of the seasonal bathymetric cycle. During summer months, depths occupied are generally less than 30 fathoms (less than 50 m) and are even in the littoral zone in some regions. Wintering depths range from 135 to 150 fathoms (270–300 m) in the eastern part of the Sea of Okhotsk (west Kamchatka), from 82 to 110 fathoms (150–200 m) off southeastern Kamchatka. and from 90 to 135 fathoms (170-250 m) in the northwestern Bering Sea.

In the south boreal region of the western Pacific (south Kurile Islands to the western shores of Korea) the seasonal migration pattern is the reverse of that in the north boreal region. There, the cod inhabit relatively shallow water during winter months (15–50 m, 8–27 fathoms). Spawning occurs from December to February, depending on locality. With approach of summer the cod move to relatively deep water (100–250 m, 55–135 fathoms).

In the region from southwestern Sakhalin to Peter the Great Bay, where there is a transition between biogeographic features of the north and south boreal regions, behaviour of the cod is intermediate between that observed to north and south.

Typical differences in the seasonal cycle of depth distribution in Pacific cod of Asia and Canada are illustrated diagrammatically in Fig. 8, with no pretence to being representative of all situations within the broad area under consideration. In Canadian waters, (1) the annual range of vertical migration is about one-third of that in the western regions of the Pacific and (2) the timing of the migration

[7]According to the biogeographic classification presented by Rass (1959: 249) waters off the west coast of Canada lie on the boundary of the north and south boreal regions of the Pacific Ocean.

appears to correspond more or less with that in the northwestern (north boreal) region.

Note in Fig. 8 that Canadian waters have been classed as north boreal. In his classification of biogeographic regions of the Pacific Ocean, Rass (1959) separates the north and south boreal regions of the northeastern Pacific near Cape Scott (northern end of Vancouver Island). More detailed study of general zoogeography in this area may show that the boundary should be somewhat farther to the south. In any event, it is probable that Canadian waters should be classed as a transition zone between the two major divisions.

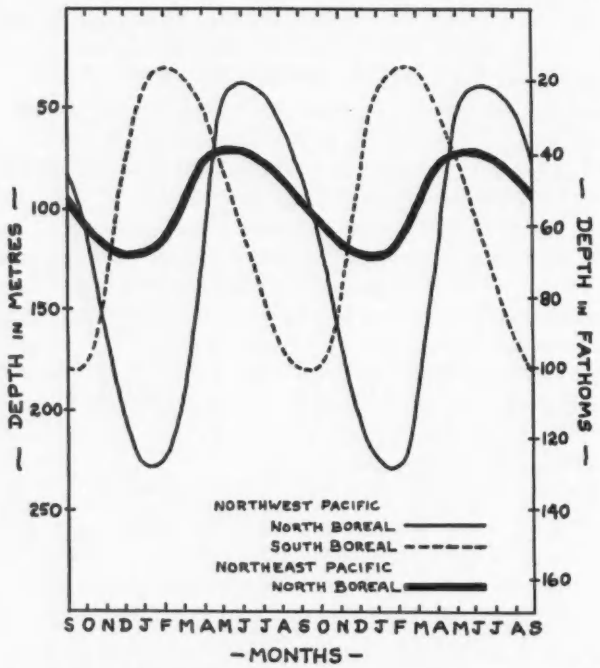

FIG. 8. Diagrammatic representation of the seasonal vertical migrations of cod in various regions of the North Pacific Ocean.

Moiseev (1953: 97) estimates that cod of the Pacific Ocean occur, broadly speaking, within the temperature range of −1.5° to +18°C. However, by eliminating situations where conditions for growth, reproduction and survival are marginal, this range can be narrowed substantially. A range of 0° to 10°C would more aptly describe the conditions under which cod flourish in appreciable numbers.

In the north boreal region of the western Pacific, cod tend to avoid areas where temperatures fall below 0°C or rise above 10°C. During the summer

months, they are to be found generally between 2° and 6°C. In the western Bering Sea, "optimum" temperatures are between 0.2° and 4.5°C during summer (Moiseev's table 66). Temperatures at time of spawning (late winter) are between 0° and 2–3°C.

In the south boreal region where the seasonal vertical migrations of cod are the reverse of those in the north, "optimum" temperatures range from 1.2° to 7.0°C. Uda (1957) suggests that near the western shores of Japan the "optimum" temperatures for cod are between 2° and 4°C. Similar temperatures are recorded by Moiseev (1953: 83) for spawning grounds in the transition areas of south-western Sakhalin and Peter the Great Bay. Near the southern limit of the cod's range off southeastern Korea, temperatures at depths occupied during summer months do not rise above 6° to 8°C, while winter temperatures are of 5°C or less (Moiseev, 1953: 99—remarks based on the work of Uchida).

It is apparent from the foregoing that Pacific cod in waters along the Asian coast generally are adapted to much lower temperatures than those off the coast of Canada. Only towards the southern limit of the cod's range (Korea) is any similarity of temperature experience to be noted.

In the North Pacific as a whole, cod occur mainly within the range of 0° to 10°C. The pattern of seasonal vertical migration appears to depend on the extent to which temperatures at the extremities of this range intrude upon or envelope the continental shelf. In the Asiatic north boreal region, pronounced migrations of cod to deep water in winter months are accompanied by intensive cooling of the upper zones of the sea (down to 0°C and less). On the other hand, migration to deep water in the summer months in the south boreal region is accompanied by rapid heating of the upper zones to temperatures well above 10°C.

In contrast to these situations we find that off the Canadian coast, seasonal changes in temperature are very moderate and that these are associated with only moderate changes in the seasonal bathymetric distribution of cod.

It is this general association between cod movements and the amplitude and timing of seasonal cycles of temperature which leads one to suspect that temperature *per se* is of over-riding importance in the geographic and bathymetric distribution of cod in the North Pacific.

OTHER BIOLOGICAL CHARACTERISTICS OF PACIFIC COD IN CANADIAN WATERS

In the foregoing section evidence was presented in support of the view that Pacific cod are adapted to conditions of relatively high temperature in waters along the Canadian coast. In such an environment there would be reason to suspect a higher rate of metabolism than in other regions of the North Pacific and that this would manifest in a higher rate of growth, earlier maturity and a

higher rate of natural mortality. It is instructive, therefore, to examine available data on these processes in Canadian cod and compare them with observations from the northwestern Pacific.

A. GROWTH RATE

As yet, no effective method has been developed for age determination of cod taken in Canadian waters. Scales and otoliths (conventional tools for age determination) appear to be unsuitable for they lack well-defined and consistent patterns of annular checks. This in itself may be indicative of a high-temperature environment, for the difficulty of age determination is not encountered to the same degree in age materials collected in colder regions of the North Pacific. Otolith and scale samples from the southeastern Bering Sea (examined by staff of the Nanaimo Station) appear to possess patterns which are representative of age[8]. Also, Mosher (1954) was able to obtain estimates of age from otolith samples collected in the same area.

Otoliths and scales have also been used by Soviet scientists working on cod of the northwestern Pacific. However, age determination of Asian cod appears to require use of both the otolith and the scale, as neither one is satisfactory by itself for all sizes of fish (Moiseev, 1953: 61).

Despite the present lack of satisfactory methods for age determination of cod in Canadian waters, some information on growth rate can be obtained from length-frequency data and from the results of tagging.

1. Growth Evident from Movement of Length Modes

For the purpose of calculations which follow it is presumed that March 1 marks the beginning of the "cod year". In the Strait of Georgia, small-meshed trawl surveys have shown that O-group cod achieve a length of 10.7 cm (range 8 to 14 cm) by mid-July. Growth rate may be somewhat greater in this region than in Hecate Strait (400 miles to the northwest) where young cod have been observed to reach a length of 8.9 cm (range 6 to 11 cm) by the same time of year.

By late autumn in the first year of life, juvenile cod in the Strait of Georgia exceed 20 cm in length. Results of sampling during the winters of 1954–55 and 1957–58 are shown in Fig. 9 (data from Table VII). These data permit an approximate estimate of the length attained at completion of the first year of growth. The average size ($\bar{x}$) and standard duration (s) of the smallest modal group on November 15, 1954 was $\bar{x} = 20.7$ cm, $s = 1.8$; on January 12, 1955 $\bar{x} = 24.1$ cm, $s = 1.9$. Graphical extrapolation to March 1, 1955, yields an estimate of 26.9 cm. Interpolation from the average size on December 17, 1957 ($\bar{x} = 21.8$ cm, $s = 2.2$) and on March 19, 1958 ($\bar{x} = 26.4$ cm, $s = 2.7$) yields a

[8]These samples have been provided through the cooperation of the staff of the International Pacific Halibut Commission and the U.S. Bureau of Commercial Fisheries (Seattle).

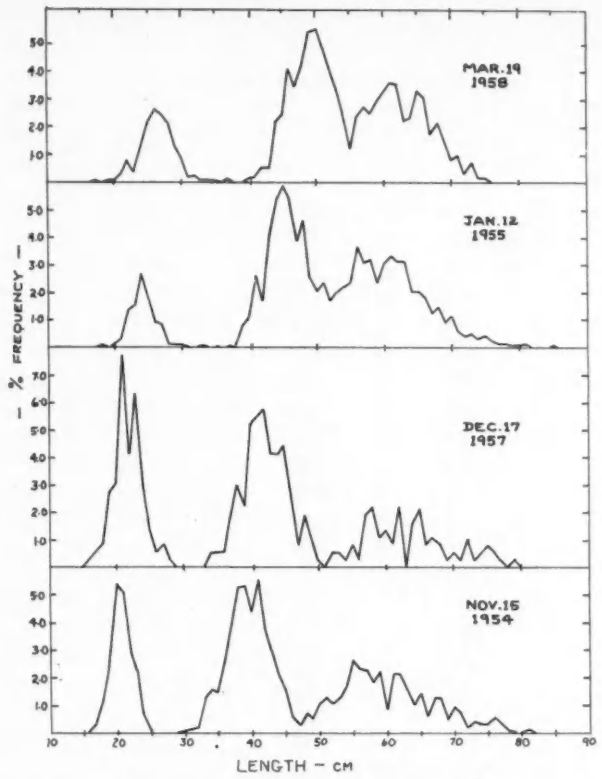

FIG. 9. Length-frequency distributions of Pacific cod taken by the research trawler M/V *Investigator No.* 1 on grounds along the east coast of Vancouver Island, Strait of Georgia.

value of 25.4 cm for March 1, 1958. The average of these two estimates is 26.1 cm, which for present purposes shall be regarded as the average length achieved at the completion of the first year of growth (Age I).

As shown in Fig. 9, another mode appears in the length-frequency distribution between lengths of about 40 cm to 50 cm. This group consisted of fish which were in the process of completing their second year of growth. Their separation from still older fish was achieved by plotting the data on probability paper, thus providing the following estimates of average length:

	Nov 15 1954	Dec. 17 1957	Jan 12 1955	Mar 19 1958
Average length (*cm*)	40.0	42.5	46.4	49.4
Standard deviation (*s*)	3.0	3.1	3.5	3.1

TABLE VII. Length-frequency distributions of Pacific cod taken on trawling grounds along the lower east coast of Vancouver Island, Strait of Georgia.

Length	Nov. 15, 1954		Dec. 17, 1957		Jan. 12, 1955		Mar. 19, 1958	
cm	*no.*	%	*no.*	%	*no.*	%	*no.*	%
16	...	...	1	0.27	...	...	...	...
17	4	0.43	2	0.55	...	...	1	0.09
18	11	1.18	3	0.82	1	0.08	...	...
19	22	2.35	10	2.75	...	...	1	0.09
20	51	5.44	11	3.02	2	0.16	1	0.09
21	48	5.12	28	7.70	4	0.33	4	0.35
22	29	3.09	15	4.12	16	1.31	9	0.80
23	22	2.35	23	6.32	19	1.56	4	0.35
24	6	0.64	11	3.02	33	2.71	13	1.15
25	1	0.11	5	1.37	21	1.72	24	2.13
26	...	...	2	0.55	11	0.90	30	2.66
27	...	...	3	0.82	10	0.82	28	2.49
28	...	...	1	0.27	1	0.08	24	2.13
29	...	...	...	...	1	0.08	15	1.33
30	1	0.11	...	...	1	0.08	10	0.89
31	1	0.11	...	...	...	...	2	0.18
32	2	0.21	...	...	...	...	3	0.27
33	12	1.28	...	...	1	0.08	1	0.09
34	15	1.60	2	0.55	...	...	1	0.09
35	14	1.49	2	0.55	1	0.08	1	0.09
36	24	2.56	2	0.55	...	...	...	...
37	38	4.06	7	1.92	1	0.08	1	0.09
38	50	5.34	11	3.02	1	0.08	...	...
39	50	5.34	8	2.20	10	0.82	...	...
40	41	4.37	19	5.22	14	1.15	2	0.18
41	52	5.54	20	5.50	32	2.63	3	0.27
42	34	3.63	21	5.77	20	1.64	6	0.53
43	28	2.98	15	4.12	50	4.11	6	0.53
44	19	2.03	15	4.12	65	5.34	24	2.13
45	15	1.60	16	4.40	72	5.91	27	2.40
46	6	0.64	10	2.75	65	5.34	47	4.17
47	3	0.32	3	0.82	47	3.86	40	3.55
48	7	0.75	7	1.92	57	4.68	48	4.26
49	5	0.53	4	1.10	31	2.55	61	5.41

TABLE VII (continued)

Length	Nov. 15, 1954		Dec. 17, 1957		Jan. 12, 1955		Mar. 19, 1958	
cm	*no.*	%	*no.*	%	*no.*	%	*no.*	%
50	10	1.07	1	0.27	25	2.05	63	5.58
51	12	1.28	...	...	29	2.38	55	4.88
52	10	1.07	2	0.55	21	1.72	46	4.08
53	12	1.28	2	0.55	25	2.05	38	3.37
54	16	1.71	1	0.27	27	2.24	27	2.40
55	25	2.67	3	0.82	29	2.38	14	1.24
56	22	2.35	1	0.27	45	3.70	27	2.40
57	21	2.24	7	1.92	38	3.12	31	2.75
58	17	1.81	8	2.20	39	3.21	28	2.49
59	21	2.24	4	1.10	29	2.38	33	2.93
60	8	0.85	5	1.37	37	3.04	37	3.28
61	20	2.13	3	0.82	41	3.37	41	3.64
62	20	2.13	8	2.20	38	3.12	40	3.55
63	15	1.60	...	...	38	3.12	25	2.22
64	10	1.07	6	1.65	25	2.05	26	2.31
65	14	1.49	8	2.20	25	2.05	38	3.37
66	6	0.64	3	0.82	23	1.89	34	3.02
67	12	1.28	4	1.10	15	1.23	20	1.77
68	12	1.28	3	0.82	18	1.48	24	2.13
69	5	0.53	1	0.27	11	0.90	17	1.51
70	9	0.96	2	0.55	14	1.15	9	0.80
71	7	0.75	1	0.27	7	0.57	11	0.98
72	2	0.21	4	1.10	5	0.41	4	0.35
73	4	0.43	1	0.27	6	0.49	8	0.71
74	3	0.32	2	0.55	4	0.33	2	0.18
75	3	0.32	3	0.82	5	0.41	2	0.18
76	5	0.53	2	0.55	3	0.25	...	...
77	3	0.32	1	0.27	2	0.16	...	...
78	1	0.11	...	...	2	0.16	...	...
79	...	...	1	0.27	1	0.08	...	...
80	...	...	...	...	...	...	...	...
81	1	0.11	...	...	2	0.16	...	...
82	...	...	...	...	...	...	...	...
82	...	...	...	...	...	...	...	...
84	...	...	...	...	...	...	...	...
85	...	...	...	...	1	0.08	...	...
Total	937		364		1,217		1,127	

As in the computation of average length at Age I, the November and January average lengths were extrapolated to March 1, yielding an estimate of 51.9 cm; the December and March averages were interpolated to obtain an estimate of 47.9 cm. The mean of these two estimates is 49.9 cm, and is here taken as an approximation of the length attained at the completion of Age II.

Although this group can be traced well into its third year of growth, overlapping with older age groups increases and makes difficult a reliable separation of the length-frequency distribution into its component parts.

2. Growth Evident from Tagging

An alternative procedure for determining growth rate of Age II and older fish is to be found in the results of tagging. As noted above, average length at completion of Age II was estimated to be 49.9 cm. If we ascribe to the frequency distribution of these fish a standard deviation of 3.2 (an average from the foregoing table), we can say that the majority of Age II fish were within the range 46.7–53.1 cm.

From 1954 to 1959 inclusive, 6,075 Pacific cod were tagged on Strait of Georgia grounds and all were released during the winter period. Within the range 46.7 to 53.1 cm, 67 fish, for which reliable information was available on growth, were recaptured one year after tagging (actually, the 11th to 13th month after release). The average length of these fish, when tagged, was 49.6 cm—for practical purposes, the same as that estimated as average length of fish which had completed Age II. The average length at recapture was 61.4 cm ($s = 4.2$) which can be taken as an approximation of the length at completed Age III. Unfortunately, recaptures after two years of freedom were so few that it was impossible to estimate length at completed Age IV from this particular group of tagged fish.

However, as an alternative, we can examine the one-year returns from fish tagged at the size estimated for Age III fish above, namely, within the range 57.2 to 65.6 cm. A total of 76 fish qualified for this treatment, and their average length at time of recapture was 66.1 cm ($s = 3.8$). However, their average length at time of tagging was only 60.3 cm, as compared with the 61.4 cm as estimated above for length at completion of Age III. Therefore, an approximate correction for the average length at completed Age IV would be $61.4/60.3 \times 66.1$ or 67.3 cm.

Of course, these are rather hazardous calculations, and they become increasingly so as we attempt to determine average lengths for the few remaining ages in the life span. Not only are the numbers of eligible tag recoveries fewer but the sex ratio beyond Age IV swings strongly in favour of female fish which presumably grow more rapidly than male fish[9]. Thus, the apparent growth rate may accelerate as the numbers of males decrease among larger fish. Further-

[9]In these growth studies based on tagging data, growth rates could not be determined for male and female fish separately. At time of tagging there is no means of determining sex, and recaptured fish are usually gutted before they are reported.

more, from Age IV onwards the standard deviations of the length distributions for the various age groups begin to overlap.

Twenty-seven tagged fish within the length range 63.5 to 71.1 cm (i.e., as Age IV with mean size 67.3 cm, $s = 3.8$) averaged 71.6 cm in length ($s = 3.8$) one year later. Again, correcting for the disparity between the actual mean length at time of tagging (66.3 cm) and that calculated for Age IV, we get $67.3/66.3 \times 71.6 = 72.6$ cm as the estimated length at Age V.

Ten fish tagged within the range 68.8–76.4 cm (Age V, 72.6 ± 3.8 cm) had an average length of 75.1 cm one year later. Their average length at time of tagging was, however, 71.5 cm. Thus, the corrected estimate of the average length at Age VI was $72.6/71.5 \times 75.1$ or 76.2 cm.

Beyond this point no further information is available because of the paucity of one-year returns from taggings of fish greater than 72 cm in length.

The foregoing calculated lengths at each age are summarized in Table VIII with estimates of the apparent average annual increment (as well as estimates of average weight and instantaneous growth rate). Data from columns 2 and 3 of this table are illustrated in Fig. 10, part (b) of which is a modification of the Walford-type relationship between length at time of tagging (l_t) and length one year after tagging (l_{t+1}). In this case, the annual increment of growth in length ($l_{t+1} - l_t$ is plotted against l_t, a graphical expression of the modified Brody-Bertalanffy equation:

$$l_{t+1} - l_t = L_\infty(1 - e^{-K}) + l_t\,(e^{-K} - 1)$$

where K is the growth coefficient and L_∞ is the asymptotic length (see Holt, 1959).

A least-squares fit to all of the data in Fig. 10b (solid line) yields $K = 0.58$ and $L_\infty = 77.4$ cm, whereas, if we consider only the first three points as being reliable (broken line in Fig. 10b), then $K = 0.71$ and $L_\infty = 72.8$ cm.

The suggestion mentioned by Ricker (1958: 195) for obtaining a better fit (by using trial values of L_∞ to find the straightest (best) line fitting the plot of values of $\log_e (L_\infty - l_t)$ against t) could be followed. However, in view of the questionable accuracy of the data, it might be more appropriate simply to fit by eye a line which provides a value of L_∞ intermediate to those given above, i.e., $L_\infty = 75.1$, whence K is found to be 0.67.

Alternatively, we may treat the tagging data less selectively by avoiding any separation into age groups. Thus in Fig. 11, increments of growth as indicated by all one-year tag returns are plotted against lengths at time of tagging. The line of best fit to these data is expressed as $Y = 324 - 0.432\ X$, whence it follows that $K = 0.56$ and $L_\infty = 75.0$. Although these values are in close accord with those derived from Fig. 10b, the limits of error are obviously quite large. The high degree of variability in values of $l_{t+1} - l_t$ is generated at least in part by differential rate of growth betwen the sexes. As mentioned earlier, it was not possible to separate the tag returns by sex. Furthermore, it is fairly obvious

TABLE VIII. Estimated growth rate of Pacific cod in Strait of Georgia waters, based on observations of length-frequency modes and on results of tagging.

1	2	3	4	5	6	7
Age (completed years)	Average length	Average increment	Average weight		Log_e(wt)	Instantaneous growth rate (g)
	cm	*cm*	*g*	lb		
I	26.1		200	0.45	5.30	
		23.8				1.99
II	49.9		1,470	3.23	7.29	
		11.5				0.64
III	61.4		2,780	6.15	7.93	
		5.9				0.25
IV	67.3		3,570	7.87	8.18	
		5.3				0.19
V	72.6		4,330	9.55	8.37	
		3.6				0.18
VI	76.2		5,180	11.42	8.55	

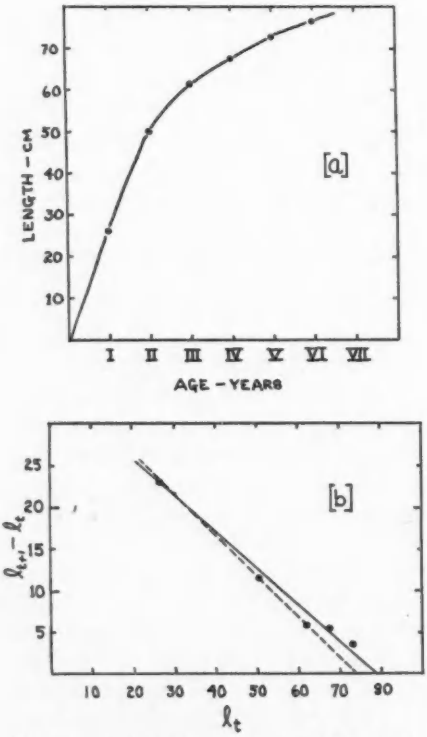

FIG. 10. Estimated growth of Pacific cod in the Strait of Georgia: (a) relation between length and age, and (b) the same data expressed as a modified Walford graph.

in Fig. 11 that the relationship between $l_{t+1} - l_t$ and l_t would be better described by a curvilinear expression rather than a linear one.

Accordingly, it must be recognized that the values of K and L_∞ as computed here, and used in a later section dealing with mortality rates, are merely approximations. Further work appears necessary in order to determine whether or not the growth rate of Pacific cod in Strait of Georgia waters is described with sufficient accuracy by the Brody-Bertalanffy equation.

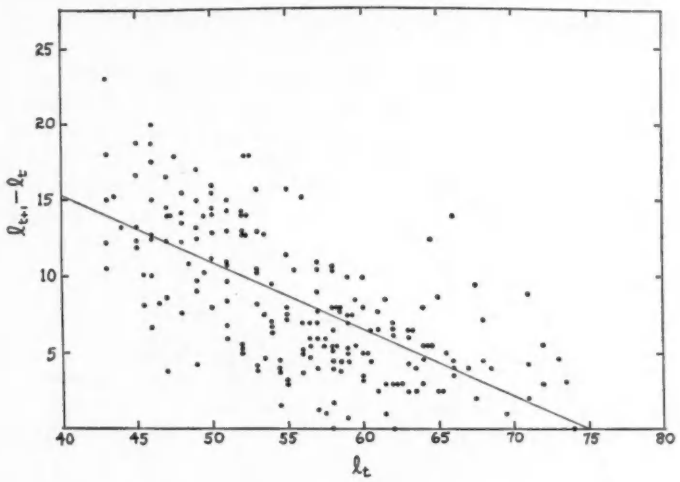

FIG. 11. A modified Walford graph showing the relation between length of Strait of Georgia cod at time of tagging (l_t) and the increment of growth after one year at large ($l_{t+1} - l_t$). Measurements in centimetres.

Further work is also required to determine whether or not the growth rate as exhibited by Strait of Georgia fish differs significantly from that in the open waters of the Canadian coast (Hecate Strait, Queen Charlotte Sound, etc.). Preliminary tagging in the Strait of Georgia (Forrester and Ketchen, 1955) resulted in only a few recaptures being made in outside waters (west coast of Vancouver Island). Subsequent taggings have revealed more emigration, but the weight of evidence still favours the conclusion that Strait of Georgia cod are more or less independent of those offshore. Nevertheless, length-frequency distributions for all areas are very similar and this would suggest that growth rate and age composition is not markedly different between inshore and offshore grounds, at least adjacent to the southern Canadian coast. As mentioned earlier, growth rate in northern (Hecate Strait) waters may be slightly slower than in the south—and this might be expected in view of the temperature difference between the two areas. Results of recent taggings in Hecate Strait must be awaited before this question can be answered with certainty.

It is instructive to compare the above observations on growth rate of Strait of Georgia cod (approximate as they may be) with similar observations in the northwestern Pacific Ocean. Such a comparison is made in Fig. 12 (data from Table IX). Information respecting cod of western Bering Sea and the Sea of Okhotsk (west Kamchatka) is taken from Moiseev (1953: 66) and is based on back calculations. Data for the east coast of Korea were obtained indirectly

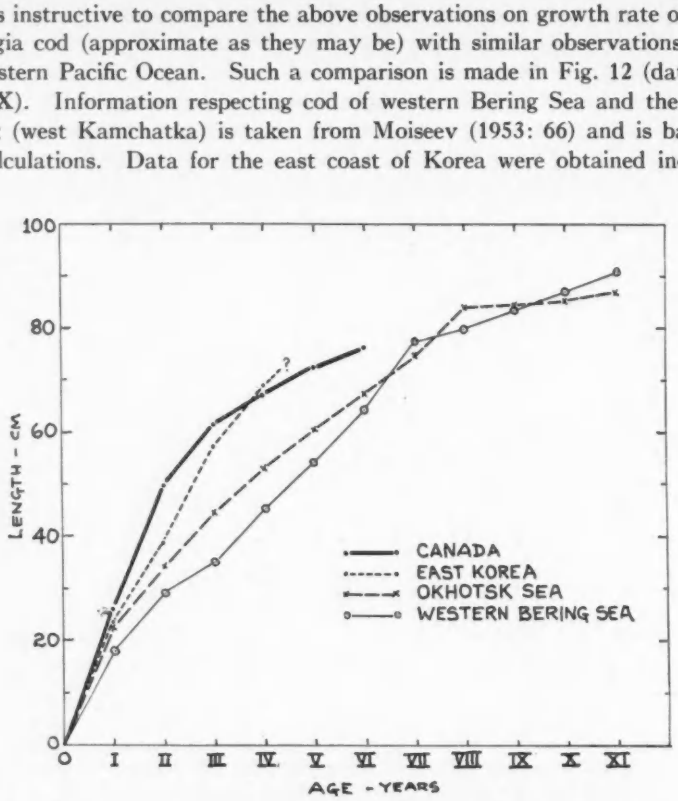

FIG. 12. A comparison of the age-length relationships of cod inhabiting various regions of the North Pacific Ocean and adjoining seas.

TABLE IX. Age-length relationships of cod from various regions of the North Pacific Ocean and adjoining seas.

	Average length (*cm*) at ages below (completed years)										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
1. *West Bering Sea* (*1933 Olyutorski Bay*)											
	18.0	29.5	35.5	45.7	54.2	64.2	77.4	79.8	83.6	87.0	91.0
2. *Sea of Okhotsk* (*1929–33*)											
	22.8	34.6	44.8	53.4	60.8	67.7	75.1	84.0	84.1	85.5	87.5
3. *East coast of Korea*											
Range	20–27	30–48	50–65	66–72	*ca* 80	*ca* 90					
Mid-point	(23.5)	(39.0)	(57.5)	(69.0)							
4. *British Columbia* (*Strait of Georgia 1954–58*)											
	26.1	49.9	61.4	67.3	72.6	76.2	?				

from a paper by Uchida (1936)[10]. As Uchida gave only the range of lengths at each age, a mean point in the range has been used in drawing the graph shown in Fig. 12.

Strait of Georgia cod appear to have a more rapid initial rate of growth than those in the three other areas considered (presuming that data for the latter are representative of present-day conditions). Although there is some uncertainty about the accuracy of the estimates beyond Age III, growth rate beyond this age becomes less than that observed in the Sea of Okhotsk and western Bering Sea. Up to Age III the rate of growth of Canadian cod is closer to that in Korean waters than in the regions farther to the north whose temperatures are less similar to Canadian waters.

For comparison, the southernmost stock of Atlantic cod along the American coast occurs off southern New England between 35° and 41°N Lat. (Wise, 1958) —much the same as the latitudes occupied by cod at the southern limit of their range in Asia (Korea). For southern New England cod, Schroeder (1930, table 44) gives the following average lengths at each age, as based on back-calculations from scale measurements:

I	17.0 *cm*	VI	78.0 *cm*
II	38.4	VII	85.3
III	52.8	VIII	91.7
IV	63.0	IX	98.3
V	70.4	X	104.2

For the first two years of age the growth rate shown is much less than that of British Columbia cod, but perhaps about the same as in Korean waters.

B. MORTALITY RATES

Because of uncertainties encountered in age determination, conventional methods of determining total mortality rate from age composition have not as yet been applied to Pacific cod in Canadian waters. Accordingly, it is necessary to rely *pro tem* on other sources of information.

1. Mortality Rate as Related to Average Length

Where information is available on growth rate and average length of fish in the catch, an approximation can be obtained of total mortality rate. In terms of the Brody-Bertalanffy growth formula, Beverton and Holt (1956: 69) derived the following expression

$$i = \frac{K(L_\infty - \bar{l})}{\bar{l} - l'}$$

where i is the instantaneous total mortality (Beverton and Holt's F + M), $\bar{l}$ is the average length of fish in the catch that are as large or larger than the first fully recruited length, l'.

[10] I am indebted to Mr F. Nagasaki of the Tokai Regional Fisheries Research Laboratory, Tokyo, Japan, for his help in abstracting pertinent information from Uchida's paper.

Within the area for which information is available on growth rate of cod (southern Strait of Georgia), one of the main fishing grounds is that at Nanoose Bay. The fishery takes place on spawning or pre-spawning concentrations of cod during the months of February and March. Routine sampling for length has been conducted on commercial trawler catches from this ground for about a decade. The average length-frequency distribution for the years 1956–60 is given in Table X.

TABLE X. Average length-frequency distribution of Pacific cod in 1956–60 trawl catches from the Nanoose Bay fishing ground in the Strait of Georgia.

Length	Frequency	Length	Frequency	Length	Frequency
cm	%	*cm*	%	*cm*	%
40	. . .	55	4.44	70	1.70
41	0.16	56	5.82	71	1.30
42	0.36	57	6.36	72	0.82
43	0.50	58	7.32	73	0.98
44	0.44	59	6.38	74	0.56
45	0.80	60	6.82	75	0.46
46	1.02	61	6.28	76	0.22
47	1.24	62	5.64	77	0.18
48	1.40	62	5.78	78	0.09
49	1.48	64	4.08	79	0.09
50	1.86	65	3.86	80	0.09
51	1.82	66	3.14	81	. . .
52	2.54	67	2.96	82	0.04
53	2.66	68	2.58	83	0.04
54	3.86	69	2.02	84	. . .

When the data are smoothed (by threes) it appears that the mode is situated at about 59 cm. To allow for still incomplete recruitment, we may estimate l' as 60.0 cm, whence it follows that $\bar{l}$ is 64.6 cm.

These values are now applied to the above expression together with the various estimates of K and L_∞ evolved on page 539. The results are as follows:

Source	K	L_∞	i	a
1 Fig. 10b	0.58	77.4	1.62	.802
2 " "	0.71	72.8	1.27	.719
3 " "	0.67	75.1	1.53	.784
4 Fig. 11	0.56	75.0	1.27	.719

In all cases the estimates of i (or a, the annual total mortality rate) are remarkably high—as high as estimates obtained from *heavily fished stocks of Pacific herring* (cf. Tester, 1955: 666). Of course, their reliability hangs heavily on the accuracy of estimates of K and L_∞, and small differences in these latter values result in a considerable difference in estimates of i (cf. i_1 and i_4).

Ricker (1958: 204) suggests that the greatest weakness of mortality estimates based on average length is that they do not detect possible age variation in

mortality rate. As will be shown in the discussion of mortality estimates from tagging, the mortality rate of Strait of Georgia cod (or at least the rate of disappearance from the fishery) seems to increase with age. This may limit the usefulness of the Beverton and Holt expression (which assumes i to be constant) even if wholly reliable data on growth rate were at hand.

A high apparent total mortality rate *might* reflect not only the rate of death due to fishing and natural circumstances but also a certain rate of permanent emigration from the effective range of fishing. Actually this is rather improbable. Canadian and United States trawler fleets operate over a range of depths which extend well above and below the depths where cod are to be found. Catches are fairly homogeneous with respect to length, and little segregation by size amongst mature fish can be detected such as would appear if the fish moved to deeper water as they got larger and older (as do blackcod, lingcod and other species).

Despite markedly different histories of exploitation, the length-frequency compositions of cod from various banks along the Canadian coast are very similar. Hence, the preliminary conclusion is that total mortality rate is of the same order of magnitude in all areas and that a large share of this is due to natural mortality. Samples collected from northern Hecate Strait in 1951, when the cod fishery was in its early stages of development, indicated a total mortality rate in excess of 60% per annum (based on the Beverton-Holt method described above). Thus, it is conceivable that annual natural mortality rate is of the order of 60% (about 0.9 on an instantaneous basis).

2. Mortality Rates Based on Tag Returns

Mature cod move in to the Nanoose Bay ground, Strait of Georgia, during the months of February and March, from southern waters of the Strait. Fishing is restricted by regulation to the period February 1 to March 20 each year. In 1955 and 1958 tagging was conducted toward the end of the open season in Nanoose Bay (Table XI). In both years, during the first 6 months after tagging relatively few recaptures were made—partly because of cessation of fishing in the tagging area and partly because of reduced fishing effort in other parts of the Strait of Georgia during the spring and summer months. The bulk of the returns came in the 7th to 12th months and within that period most came during the 11th and 12th months on the Nanoose Bay ground.

Survival rates, based on first and second year recaptures from each tagging are shown in the following tabulation. Allowance for differences in fishing effort (Table XII) has been made in the adjusted second year recaptures.

Year of tagging	1st year recaps	2nd year recaps	Adjusted 2nd year recaps	Survival rate s	Inst. total mortality rate i
1955	82	12	14	.171	1.77
1958	43	11	10	.233	1.46

TABLE XI. Recaptures from cod tagging conducted at Nanoose Bay in March 1955 and March 1958. Column 1 indicates size range at tagging.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	1955 tagging					1958 tagging					Combined taggings				
		Numbers of recaptures					Numbers of recaptures					Numbers of recaptures			
Length group (*cm*)	Numbers tagged	1–6 mo.	7–12 mo.	13–18 mo.	19–24 mo.	Numbers tagged	1–6 mo.	7–12 mo.	13–18 mo.	19–24 mo.	Numbers tagged	1–6 mo.	7–12 mo.	13–18 mo.	19–24 mo.
<41	2	...	...	...	...	...	...	...	...	...	2	...	...	...	...
41–45	7	...	1	...	...	10	...	...	...	...	17	...	1	...	...
46–50	25	...	3	...	...	71	2	5	—	—	96	2	8	—	—
51–55	65	3	8	—	3	95	3	3	—	1	160	6	11	—	4
56–60	171	4	19	2	1	161	2	12	1	1	332	6	31	3	2
61–65	177	5	21	1	2	188	3	6	—	1	365	8	27	1	3
66–70	117	6	5	—	—	106	4	1	—	—	223	10	6	—	—
71–75	44	2	5	3	—	27	1	1	—	—	71	3	6	3	—
76–80	8	—	—	—	—	5	—	—	—	—	13	—	—	—	—
>80	3	—	—	—	—	1	—	—	—	—	4	—	—	—	—
Unclassified		—	—	—	—		—	—	—	(7)		—	—	—	(7)
Totals	619	20	62	6	6	664	15	28	1	(10)	1,283	35	90	7	(16)
		82		12			43		(11)			125		(23)	

TABLE XII. Statistics of total fishing effort (hours of trawling) in the southern part of the Strait of Georgia.

	Year and period							
	1955	1955–56	1956	1956–57	1958	1958–59	1959	1959–60
Area	Apr-Sept	Oct-Mar	Apr-Sept	Oct-Mar	Apr-Sept	Oct-Mar	Apr-Sept	Oct-Mar
Gulf Islands	1,519	5,364	2,150	4,089	1,086	4,493	1,001	4,957
Nanoose Bay	. . .	462	. . .	327	. . .	507	. . .	732
Totals	1,519	5,826	2,150	4,416	1,086	5,000	1,001	5,689
	7,345		6,566		6,086		6,690	

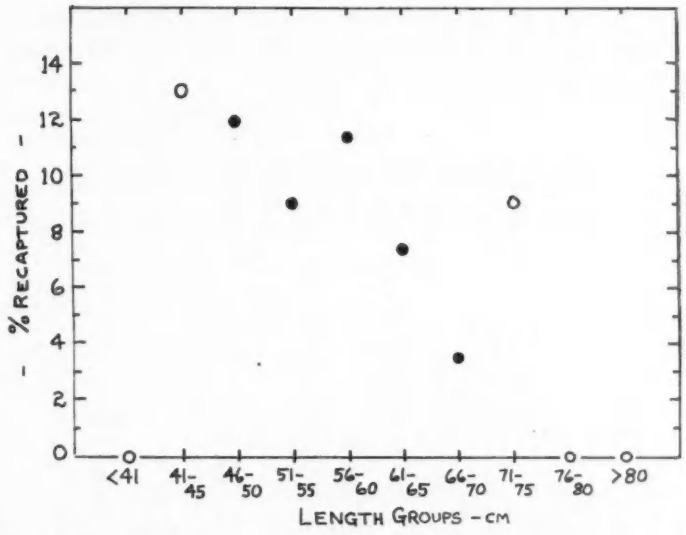

FIG. 13. Percentage returns from various tagged length groups of cod, 7 to 12 months after tagging at Nanoose Bay, Strait of Georgia (data from Table XIV). Open circles indicate recaptures from fewer than 100 tagged fish.

This analysis probably puts an upper limit on the estimates of i. Some allowance was made for the loss of tags through shedding, but this factor could not be corrected for entirely. Shedding is known to have occurred in the tags used at Nanoose Bay, particularly in 1958[11]. In addition, the observed decrease in tag returns with size (Fig. 13) suggests a bias in the direction of greater than

[11]Since 1955, various types of tags have been used: polyvinyl (spaghetti) tubing, monofilament and braided cord of nylon and other synthetics. In 1958, only polyvinyl tubing was used at Nanoose Bay. No shedding was apparent until the second year when a number of broken tags were reported (the "unclassified" tags in Table XI). Although these lacked identifying serial numbers, it was presumed that they originated from the 1958 tagging. These broken tags were still fused to the fish when captured. Presumably others did not remain attached.

representative mortality because the fish were two years older by the time the final returns were in.

A weighted average of the two estimates of i (1.68) was obtained by pooling the first and second year recaptures from the two taggings and weighting these to the pooled fishing effort.

In spite of the likelihood that this is an overestimate of total mortality rate, it is instructive to consider briefly a method of partitioning the component rates of fishing and natural mortality, based on the hypothesis that (1) natural mortality is at a uniform instantaneous rate throughout the year, and (2) that the instantaneous rate of fishing mortality varies as fishing effort throughout the year. Dr W. E. Ricker has suggested the following procedure:

Combined first-year recaptures from the 1955 and 1958 taggings are assembled by quarter-year periods (1 to 4) in Table XIII, together with data on total fishing effort (from Table XII).

TABLE XIII. First-year tag returns by quarters from the March, 1955 and March, 1958 cod taggings at Nanoose Bay and associated statistics of fishing effort for the southern part of the Strait of Georgia.

	Period			
	1	2	3	4
	Apr-Jun	Jul-Sept	Oct-Dec	Jan-Mar
Tag returns				
1955 tagging	11	—	8	18
1958 tagging	18	6	16	48
Totals	29	6	24	66
	35		90	
Hours of fishing				
1955	1,519		5,826	
1958	1,086		5,000	
Total	2,605		10,826	

Fishing effort in the first two periods $f_{1+2} = 2{,}605$ hours, and $f_{3+4} = 10{,}826$ hours. On the basis of the ratio of recaptures in periods 3 and 4, i.e., 24:66, we estimate that $f_3/f_4 = 1/2.75$, whence $f_3 = 2{,}887$ hours and $f_4 = 7{,}939$ hours[12].

Assuming that hours of fishing measure effective effort, then the instantaneous rate of fishing mortality is proportional to fishing effort (f). Hence:

$$\frac{p}{13431} = \frac{p_1+p_2}{2605} = \frac{p_3}{2887} = \frac{p_4}{7939}$$

[12]It would have been better to use the actual fishing effort by quarters but these statistics were not readily available.

If we take a trial value $q = 1.20$ for the instantaneous natural mortality rate, then the corresponding trial value of p is $1.68 - 1.20$ or 0.48. Thus for Periods 1 and 2 we have the following:

$$\text{trial } p_1 + p_2 = \frac{2605}{13431} \times 0.48 = 0.09$$

$$\text{trial } q_1 + q_2 = \frac{1.20}{2} = 0.60$$

$$\text{trial } i_{1+2} = 0.09 + 0.60 = 0.69$$

The expected recaptures in Periods 1 and 2 are equal to the number tagged multiplied by:

$$(p_1 + p_2)\frac{a_{1+2}}{i_{1+2}}$$

In this particular case, 1,283 cod were tagged. Of this number, 93% (1,193) were classed as being in good condition at time of tagging. This number will be used as an approximate correction for initial tagging mortality. Thus, using the trial values above:

$$\text{Expected recaptures} = 1193 \times 0.09 \times 0.7224 = 78$$

From this it follows that at the end of Period 2 the survivors, S_2, are:

$$S_2 = 1193 \times e^{-i_{1+2}} = 598$$

For Period 3:

$$\text{trial } p_3 = \frac{2887}{13431} \times 0.48 = 0.10$$

$$\text{trial } q_3 = \frac{1.20}{4} = 0.30$$

$$\text{trial } i_3 = 0.40$$

$$\text{Expected recaptures} = S_2.p_3.\frac{a_3}{i_3} = 49$$

$$\text{Survivors} = S_3 = 598 \times e^{-i_3} = 401$$

Similarly, for Period 4:

$$\text{trial } p_4 = \frac{7939}{13431} \times 0.48 = 0.28$$

$$\text{trial } q_4 = \frac{1.20}{4} = 0.30$$

$$\text{trial } i_4 = 0.58$$

$$\text{Expected recaptures} = S_3.p_4.\frac{a_4}{i_4} = 85$$

Under this scheme (using trial $q = 1.2$) $78 + 49 + 85$ or a total of 212 recaptures would be expected during the first year. The actual number, however, was $35 + 24 + 66$, or 125.

Trials with other values of q soon lead to an approximation of this latter number. Thus, when $q = 1.39$ (and $p = 0.29$) the expected number of recaptures was 126. However, the seasonal distribution could be duplicated with only partial satisfaction (47, 29 and 50).

Of course this high value of q (1.39, or 75% expressed as an annual rate) is probably a maximum estimate. Initial tagging mortality, incomplete correction for unreported tag recaptures and tag loss through shedding all lead to underestimation of p, while the last-named factor leads to overestimation of i; hence q ($=i-p$) tends to be overestimated.

Values of i obtained by the two separate taggings of 1955 and 1958 were 1.77 and 1.46, respectively. Although seemingly quite high, they were of about the same order of magnitude as those determined from the average size of fish in the catch (p. 544). While some confidence is to be gained from this agreement, it is possible that the latter method too may embody sources of error which overestimate the total mortality coefficient.

Mention was made previously of the possibility that total mortality rate of cod may vary with age, and hence may render unsuitable the Beverton-Holt method for estimating total mortality rate from length-frequency distribution. It seems worthwhile to examine the evidence on this point before proceeding to other subjects.

Table XIV summarizes the first year returns by length groups from tagging conducted at Nanoose Bay in March of 1955, 1958 and 1959. The numbers of tagged fish in each length group which were recaptured during the first 6 months after tagging were subtracted from the numbers tagged to obtain an estimate of the maximum number at large at the beginning of the 7th month. Recaptures during the 7th to 12th months were then expressed as a percentage of the maximum number at large and plotted in Fig. 13. While there is a limited range of size

TABLE XIV. Summary of first-year returns from taggings of Pacific cod at Nanoose Bay in the month of March in 1955, 1958 and 1959.

1	2	3	4	5	6
Length group (*cm*)	Number tagged	Recaptures 0–6 months	Max. at large beginning of 7th month	Recaptures 7–12 months	Col 5 / Col 4
<41	5	0	5	0	0
41–45	23	0	23	3	0.130
46–50	132	6	126	15	0.119
51–55	318	11	307	28	0.091
56–60	622	14	608	70	0.115
61–65	485	11	474	35	0.074
66–70	247	0	247	9	0.036
71–75	80	2	78	7	0.090
76–80	15	0	15	0	0
>80	4	0	4	0	0
Total	1,931	44	1,887	167	0.089

groups possessing sufficient data, a downward trend in percentage recaptures is evident in size groups greater than 41–45 cm. At present there is no way of differentiating between the size-related effects of (1) decreasing availability to the fishery and (2) increasing natural mortality rate. However there is a lack of evidence of permanent emigration from the fishery (p. 545) and, although its occurrence may be difficult to detect, one is left with the suggestion that natural mortality rate increases with age.

C. AVERAGE AND MAXIMUM LENGTHS OF COD

The Pacific cod is of relatively small size in the southern part of its range along North America. This is one reason why the salt fish fishery of the early days (which depended on large fish) failed to develop closer than it did to ports of landing in the United States. Cobb (1927: 389, 400) makes note of the small size of cod on banks from Kodiak Island southeastward to Dixon Entrance.

In Canadian waters the largest cod ever caught, according to Clemens and Wilby (1946), was 3 feet 3 inches in length (about 99 cm). The largest fish recorded in sampling conducted by the Fisheries Research Board during the past decade was 93 cm (two specimens taken on the Goose Island Bank in May, 1955, between depths of 36–57 fathoms). Another specimen 91.5 cm in length and weighing 21.8 lb (round) was captured off the estuary of the Fraser River in February, 1955. Such records are very rare and, indeed, specimens greater than 80 cm in length are rather uncommon. The length-frequency distribution given in Table X is rather typical of the trawl catches from Canadian waters. The modal length is usually in the vicinity of 60 cm (approximately 6 lb round wt) which, as mentioned earlier, is approximately the length achieved by 3 years of age.

It is evident from the comments of Cobb (1927: 388, 444) that cod taken in the early days by the line fishery in western Alaska were of substantially larger size than those taken in Canadian waters. Average round weight in the catch during a 4-year period was 11.25 lb (average length probably between 75 and 80 cm). Largest specimen recorded by Cobb was one weighing 40 lb and measuring 43 inches (about 110 cm) in length.

For waters of the northwestern Pacific, Moiseev (1953: 45) states that cod do not exceed a length of 115 cm and a weight of 18 kg (about 40 lb), and he points out that Pacific cod do not achieve as large a size as Atlantic cod. According to Moiseev's table 10, the average length of cod taken with various types of fishing gear in western Kamchatka waters between 1929 and 1939 was 78.9 cm—probably rather similar in size composition to the cod which were the object of fishing in western Alaska waters in early days.

The foregoing remarks are intended merely as a general comparison of the sizes of cod in various sectors of the North Pacific. Detailed comparisons are not possible because of the different histories of exploitation and different types of gear used.

D. LENGTH AND AGE AT MATURITY

In Strait of Georgia waters, male and female cod reach sexual maturity at different length and age. Fifty per cent of male fish reach maturity at a length of 48 to 49 cm, which corresponds to an age of 2 (completed) years. Apparently all are mature by 3 years. Only 15% to 25% of female fish are mature by the time they reach Age II, but almost all are mature at Age III. The 50% maturity level is at 55 cm.

Recent studies in northern Hecate Strait showed that 50% of male fish were mature at 49 to 50 cm, while the 50% level was at 55 cm in females—essentially the same as that observed in the Strait of Georgia.

In contrast, cod inhabiting waters off the west coast of Kamchatka (Sea of Okhotsk) mature at a much greater size and age. Calculations based on data presented by Moiseev (1953: table 41) suggest that 50% of male cod are mature at about 70 cm, with a corresponding length of 73 cm for females. These lengths correspond to Age VI (Moiseev's table 42). Moiseev states that the earliest age at which cod reach sexual maturity is 5 years, and that some are still immature at Age IX.

Information available from the work of Uchida (see footnote 10) implies that the cod of eastern Korea first reach maturity at Age III and that the majority are mature by Age V. If so, there is further evidence to suggest that Pacific cod in Canadian waters are biologically more comparable to those of Korean waters than those in the north boreal region of the Asian coast.

E. REPRODUCTIVE POTENTIAL

Although information is lacking which would allow quantitative determination of relative abundance of cod in various regions, it appears that they occur in lesser numbers in Canadian waters than in colder regions to the northwest. Similarly along the Asian coast, abundance apparently decreases from north to south. Conceivably, one reason would be that progressing southward from the region of maximum abundance, environmental conditions become decreasingly favourable for survival of the eggs and larvae. Alternatively, or more likely additionally, there might be a decrease in the reproductive potential—that is, a decrease in the number of eggs spawned per given number of mature fish. Thus the reproductive advantage gained by early maturity in Canadian waters above might be offset by (1) the short life span and (2) a relatively small number of eggs produced per fish at first maturity, if we presume that fecundity is a function of body weight.

In Table XV the length-frequency distribution of 1,000 mature female cod from Nanoose Bay (considered to be fairly typical of spawning populations off the Canadian coast) is compared with that of a similar number of mature females from waters off the west coast of Kamchatka. Data for the latter were obtained from Moiseev (1953: Table 41).

TABLE XV. Length-frequency distribution (per mille) in a typical spawning stock of female Pacific cod in Canadian waters (Nanoose Bay) as compared with that in waters off the west coast of Kamchatka (the latter adapted from Moiseev 1953: table 41).

Length group *cm*	Frequency		Length group *cm*	Frequency	
	Nanoose Bay	West Kamchatka		Nanoose Bay	West Kamchatka
40–44	2	. . .	75–79	19	164
45–49	13	. . .	80–84	4	124
50–54	46	. . .	85–89	. . .	144
55–59	305	16	90–94	. . .	136
60–64	335	32	95–99	. . .	64
65–69	194	100	100–104	. . .	8
70–74	82	212			

As yet no information has been obtained on the fecundity of cod in Canadian waters, so in order to compare the reproductive potentialities of the two groups, it is necessary to assume that the fecundity-length relationship in the two regions is about the same, and employ data provided by Moiseev (his table 51). These data, although few in number, provide the following expression of the relationship between fecundity and total length:

$$\hat{Y} = 0.0135X + 5.370$$

where X is the fish length in cm, and $\hat{Y}$ is the $\log_{10}$ of the number of eggs.

With the aid of length-frequency data for the two areas, it is now possible to estimate the fecundity of the two groups of fish, viz, 1.64×10^9 eggs for the Strait of Georgia (Nanoose Bay) and 2.93×10^9 eggs for western Kamchatka. Thus, for a given number of mature fish the potential egg production of Kamchatka fish is almost twice as great as that of Strait of Georgia fish—and this can be attributed to the larger size at first maturity and the longer life span.

The assumption that the fecundity-length relationship computed above for Kamchatka waters applies to Strait of Georgia cod is, of course, rather critical. According to Beverton and Holt (1957: 62), egg size within most marine fish seems remarkably constant, but there may be some exceptions (and also exceptions to the rule that fecundity is approximately proportional to body weight). In the light of Moiseev's data, it would appear that the Pacific cod, at least in the region of Asia, is one of these exceptions. A simple proportionality between fecundity and weight is not evident and apparently egg size is not constant from area to area. Moiseev presents data (his table 52) which suggest that cod of given weight (or length?) in waters off western Sakhalin produce 1.5 to 1.9 times as many eggs as cod from western Kamchatka. In this regard, Moiseev (p. 77) quotes a rule propounded by Rass (1941) to the effect that size of the cod egg increases to the northward and hence the number of eggs produced per given fish weight decreases.

The need for a test of this rule in the northeastern Pacific is apparent. If egg number per unit weight of fish (or weight of ovary) varies with latitude by

as much as a factor of 1.5 to 1.9, then it is possible that the difference in reproductive potential suggested in the discussion of Table XV would be largely negated. It remains to be determined whether or not the size of egg (and hence numbers of eggs) produced by cod in Canadian waters effectively compensates for the small size at maturity and the relatively short life span.

DISCUSSION

Although much remains to be learned about the biology of the Pacific cod in Canadian waters, it is evident that this particular geographic race or population is adapted to relatively high environmental temperatures. Furthermore, and in accordance with what can be regarded as a general rule, cod in Canadian waters are smaller than their kin in cooler regions of the North Pacific, but at the same time their growth rate in the first few years of life is more rapid. These fish mature at a relatively early age and appear to have a high annual death rate, much of which probably can be attributed to natural causes. Amongst commercially important representatives of the genus *Gadus* (viz. *G. morhua*, *G. macrocephalus*) these are unusual characteristics deserving further study and more accurate description.

Recently, Beverton and Holt (1960: 164) made a preliminary attempt to establish a relationship between the growth coefficient K and the natural mortality coefficient M (or q, as used in this paper) for the Gadiformes and other groups of fishes. Although data for the gadiform fishes (cod, haddock, coalfish, hake, etc.) are rather sparse, it appears that if we apply the K values of 0.56 to 0.71 (from page 544) to Beverton and Holt's figure 6, estimates of q are obtained which range from about 1.3 to 1.7. Beverton and Holt attach no statistical significance to their line relating values of K and q, but the above values (1.3–1.7) of q for Pacific cod in Canadian waters bracket the estimate obtained from tagging data (q = 1.39, from page 550). Because of errors inherent in the tagging method the latter estimate must still be regarded as too high, but the primitive length composition data suggest that the true figure could be as high as 0.9 at least.

Further confirmation of the relatively high value of K and q will be required before detailed consideration can be given to their significance in fishery management. However, if the preliminary results are of the right order of magnitude, it is apparent without recourse to population models that maximum yield from a year-class will be achieved by exposing it to fishing at an early age. As shown in Table VIII the instantaneous rate of growth between Ages I and II is estimated as 1.99 and between Ages II and III as 0.64. If q were as high as 0.9, then we find by interpolation that the *critical size*, namely, the average size at which instantaneous natural mortality rate equals instantaneous growth rate, comes at about Age II (average size 50 cm). In other words, it is at Age II that a cod year-class reaches its greatest bulk. In the Strait of Georgia, the minimum market size for cod is 18 inches (about 46 cm) and a substantial segment of the catch from some of the grounds consists of two-year-olds. Upward revision of the minimum market size presumably would reduce the potential yield from

a year-class, and this would be of advantage only if it were certain that the spawning stock had been reduced to a size which jeopardizes maximum production of recruits.

It is to be expected also that, in consequence of the high natural mortality rate (short life span), annual fishing success would depend heavily on the numerical strength of incoming year-classes and, therefore, would be relatively unstable. This is indeed apparent in the cod fishery along the Canadian coast—and the northern Hecate Strait fishery serves as a good example. Seasonal (January-April) average catch per hour of fishing by Canadian Class III trawlers (25–49 gross tons), as shown in the following tabulation, has varied substantially during the brief history of fishing. In 1956, catch per hour averaged less than 600 lb, but within the short space of two years it rose to more than 1,500 lb. Corresponding to these changes the total Canadian and United States catch of cod from northern Hecate Strait rose from 3,340,000 lb in 1956 to 11,240,000 lb in 1958.

Year	Average lb/hour	Year	Average lb/hour
1951	1960	1956	585
1952	1000	1957	885
1953	690	1958	1560
1954	940	1959	1105
1955	765	1960	775

Similar instability has been noted in the Nanoose Bay fishery (Strait of Georgia) where average fishing success has varied from as little as 205 lb per hour in 1955 to as high as 710 lb in 1959.

While variations in recruitment probably account in large measure for these annual variations in fishing success, they are not the only factor. It is obvious from discussions with fishermen that cod vary in *availability*[13], which affects the year-to-year success of fishing. Cod congregate and move in shoals of varying density. Not always will they inhabit bottom which is smooth enough to permit trawling, and of course there may be times when they rise off the bottom and hence escape capture by conventional fishing methods. These variations in availability are difficult to detect and even more difficult to explain. Presumably they are related in some way to the ecological requirements of the cod or of the forage animals which comprise their diet.

As described earlier, the vertical migrations of cod appear, in a general way at least, to be associated with the seasonal cycle of temperature. If cod are adapted to a fairly narrow temperature range, then presumably, they will respond by moving away when confronted with intrusions of water having temperatures much above or below this range. Frequently, fishermen report the sudden disappearance of cod from fishing banks. If these disappearances are of long duration in a fishing season then, obviously, fishing success (average catch/effort) would be an inaccurate reflection of abundance and, as such, would

[13]Availability is here defined as the fraction of the total number of individuals in the fishable size range which, during the fishing season, becomes exposed or vulnerable to the fishing gear.

lead to erroneous estimates of year-class strength or recruitment. This problem would be more serious in the case of short-lived species than in ones which have a relatively long life span in the fishery. Thus, measurement of the strengths of cod year-classes in British Columbia waters is expected to be a difficult task, even if a solution is forthcoming on the more fundamental problem of age determination!

SUMMARY

The Pacific cod is widely distributed in the cooler regions of the North Pacific Ocean and adjoining seas. In waters off the Canadian coast the cod, close to the southern limit of its range, appears throughout the year to occupy depths where the water temperature is between 6° and 9°C—considerably warmer conditions than in regions farther to the north and west.

There is a seasonal vertical migration (deep in winter and shallow in early summer), but the seasonal variation in depth is of only moderate amplitude in comparison with that observed off the coast of the USSR. This difference appears to be a reflection of the difference in amplitude of the seasonal temperature cycle in the two regions.

Estimates of age and growth are dependent entirely on observations of length-frequency modes and on results of tagging, for as yet no satisfactory method has been evolved for determining age of individual fish from scales, otoliths or other hard parts.

Apparently in consequence of the relatively high environmental temperatures off the Canadian coast, the cod has a relatively rapid growth rate during the first two years of life and a short life span. Various estimates of the growth coefficient K range from 0.56 to 0.71 for Strait of Georgia waters and estimates of L_∞, the asymptotic length, range from 72.8 to 77.4 cm.

Instantaneous total mortality rates as determined from average size of fish in the catch range from 1.27 to 1.62, while estimates from tagging range from 1.46 to 1.77. These are likely to err on the high side. Likewise, a single estimate of 1.39 for instantaneous natural mortality rate is probably too high, but there is good reason to believe that death from natural causes features heavily in the total mortality rate and that it may be over 0.9.

Sexual maturity is reached at two to three years of age—several years in advance of cod in colder regions of the Pacific Ocean. It is suggested that because of this early maturity and a relatively short life span, mature fish in a typical spawning stock of Canadian cod may be only half as fecund as those in a typical stock from northwestern Pacific waters.

ACKNOWLEDGMENTS

I am indebted to Dr W. E. Ricker for his assistance in designing the analysis of tag returns and to Dr R. R. Parker, Mr Shoichi Tanaka and Mr D. L. Alverson for their helpful criticisms of the manuscript.

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Two Epidemics of Apparent Kidney Disease in Cultured Pink Salmon (*Oncorhynchus gorbuscha*)[1,2]

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ABSTRACT

Two epidemics of a severe disease in cultured, juvenile pink salmon (*O. gorbuscha*) are described. The symptomatology of the disease and the morphology of the stained bacteria found in tissue lesions suggest that the fish were affected by "kidney disease". If the presumptive diagnosis is correct, this report is the first record of kidney disease occurring in pink salmon.

INTRODUCTION

There have been widely distributed epidemics of so-called "kidney disease", a chronic bacterial infection, in populations of most salmonids, and this insidious disease appears to be on the increase. Kidney disease has been studied extensively and the early literature reviewed by Earp *et al.* (1953), so that the present review will emphasize subsequent work. Common symptoms of the disease in young fish include the presence of macroscopic grey-white lesions, pustules and necrotic areas in and on the major internal organs, particularly the kidney (hence the name "kidney disease"), and in its terminal stages, a general bacteremia. In adult chinook salmon (*O. tshawytscha*) the liver and spleen are the primary sites of infection (Wood and Wallis, 1955). Externally, the infected fish may appear normal, or have small blisters on its sides, or the abdomen may be swollen by the intraperitoneal effusion of fluid resulting from renal damage. There may also be exophthalmos. In addition, petechiae may appear on heavily infected individuals, particularly around the vent and pelvic and pectoral fins (Earp *et al.*, 1953; Wood and Wallis, 1955). In any epidemic the syndromes seldom, if ever, involve all of these symptoms.

Microscopically, the affected areas are found to contain large numbers of Gram-positive diplobacilli, 0.3–0.5μ by 0.5–1.0μ, which have been established as the etiological agent (Earp *et al.*, 1953; Ordal and Earp, 1956). The organism is aerobic, non-motile, non-acid fast, non-capsulated and asporogenous and is fastidious in its growth requirements. Ordal and Earp (1956) tentatively identified the diplobacillus as a species of *Corynebacterium* but its taxonomic position is still in doubt.

Histologically, the disease is characterized as a systemic granuloma with the bacteria concentrated both intracellularly and extracellularly in the granulomas (Wood and Yasutake, 1956).

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The natural mode of transmission of the disease, portal of entry and source of the pathogen are still unknown (Wolf, 1958) but artificial infections in salmon have been caused by feeding naturally contaminated food (Wood and Wallis, 1955). However, trout (*S. fontinalis*) could not be infected in this manner (Snieszko and Griffin, 1955; Wolf and Dunbar, 1959), and there appears to be a complex host-parasite relationship in all salmonids. The disease can occur at a low level over a wide range of water temperatures but often increases explosively as water temperature rise. No completely effective treatment exists although various sulfonamides can retard the spread of the disease (Rucker *et al.*, 1951; Snieszko and Griffin, 1955; Wood and Wallis, 1955).

Rucker *et al.* (1954) stated that "Little opportunity is offered for the study of the possible occurrence of the disease in chum and pink salmon since these species remain in fresh water for only a short period before migration to the sea" (p. 301). Such an opportunity was afforded when we were able to culture numbers of pink salmon for an extensive period, not having suffered the usual loss of the stock due to "pin head" formation and other causes. The purpose of this paper is to report what appears to be the first (presumptive) record of kidney disease in pink salmon.

MATERIALS

The fish were hatched from eggs obtained at the Puntledge and Tsolum Rivers on Vancouver Island, and as soon as the alevins started feeding they were placed in salt water. Flowing water was used to keep the fish active during development. When the fish were about 5 to 8 cm long, they were cultured at a level of one fish to 6 gallon (27 litres), so that they were not crowded.

The diet consisted of a mixture of canned salmon, ground beef liver, dried yeast, Pablum and salt. During the first month the diet included frozen brine shrimp which were fed to demand 8 times a day.

RESULTS AND DISCUSSION

1959 Hatch, Puntledge River

Typical syndromes of kidney disease were noted in late September of 1959. Mortality rate remained at 2 to 4% per day during the next two months when the rate jumped briefly to 10 to 15% per day despite treatment with sulfamerazine according to the recommendations of Wolf (1958). The stock was then discarded. The fish had reached a mean fork length of 20 to 25 cm. Water temperatures ranged from 5 to 16°C during the period of culture.

1959 Hatch, Tsolum River

Typical syndromes of kidney disease reappeared in March, 1960, in this stock but the mortality rate was only 2 to 4% per week. However, in view of the previous failure to treat the disease successfully, it was decided to kill and examine all of the individuals in the hope of gaining some useful data. This was done on

April 14 and some of the results are shown in Table I. The actual incidence of disease was probably higher than recorded because the presence of disease was determined only by the detection of macroscopically visible lesions, although the pathogen may be present in considerable numbers even when there are no visible lesions (Wood and Wallis, 1955). Both sexes appeared equally sensitive to the disease and there was no significant difference ($P>0.5$) between the weights and lengths of healthy or diseased fish of either sex. This might indicate that

TABLE I. Sex and mean lengths and weights of healthy and diseased pink salmon, as distinguished by the absence or presence of visible lesions on major organs. Water temperature was at a peak of 11°C at the time of sampling.

Condition	Number of fish	Sex	Mean length	Standard deviation	Mean weight	Standard deviation
			cm	*cm*	*g*	*g*
No kidney	25	♀	204	17	117	38
disease	26	♂	208	17	122	39
Kidney	16	♀	204	13	118	22
disease	16	♂	209	19	124	37

infected fish continued to feed normally at least during the incipient stages of this slow-developing disease. There were no large increases of peritoneal fluid, therefore, it is unlikely that weight losses in body tissue were masked.

Healthy and diseased fish are shown in Figs. 1 and 2 respectively. Apart from the swelling on the caudal peduncle and the small blisters on the skin, there was no external difference. Most of the other diseased fish showed no external symptoms. Internally, however, diseased fish had marked grey-white lesions and necrotic areas on the liver and spleen but particularly on and in the kidney. Normal and diseased kidneys are shown in Figs. 3 and 4. A few living fish even had cardiac lesions and others were suffering such extensive tissue damage that it is surprising they survived. Translucent false membranes were found sometimes on the heart and spleen (Snieszko and Griffin, 1955). The organs first showing lesions were usually the spleen and liver.

The lesions and necrotic areas were found to contain masses of minute (0.5–0.7μ by 0.8–1.1μ) Gram-positive rods, many of which occurred in pairs. Microorganisms from the kidneys of 3 infected fish are shown in Fig. 5. The organisms were non-motile, non-sporeforming, non-acid fast (Ziehl-Neelsen) and non-capsulated (Muir's method). The cells showed little differentiation when treated with Loeffler's methylene blue or Albert's stain.

There are no indications how the pathogen was introduced into the culture or how it was transmitted, but it is doubtful if the organism came from the feed. Nutritional inadequacies of the diet might have made the fish susceptible to infection, but comparable stocks of chum (*O. keta*), coho (*O. kisutch*) and sockeye (*O. nerka*) were fed the same diet, yet only two or three coho died apparently from kidney disease. This suggests that these cultured pink salmon might

have an inherent predisposition to the disease. It has been suggested that the disease might be transmitted *via* infected eggs, "carrier" fish or both (Wolf, 1958) and/or by the salmon poisoning fluke (*Nanophyetus salmincola*) (Earp *et al.*, 1953; Snieszko and Griffin, 1955). The debilitating effects of other parasites might also be responsible for initiating this disease (Wood and Yasutake, 1956).

It is likely that this disease affects natural stocks of all salmon but the consequences are still unknown. The scope of a disease in natural populations, particularly of aquatic creatures, is usually very difficult to assess and might appear quite limited because the victims, our "statistics", are soon removed from view by physical and biological agents.

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FIGS. 1, 2, 3, 4 and 5

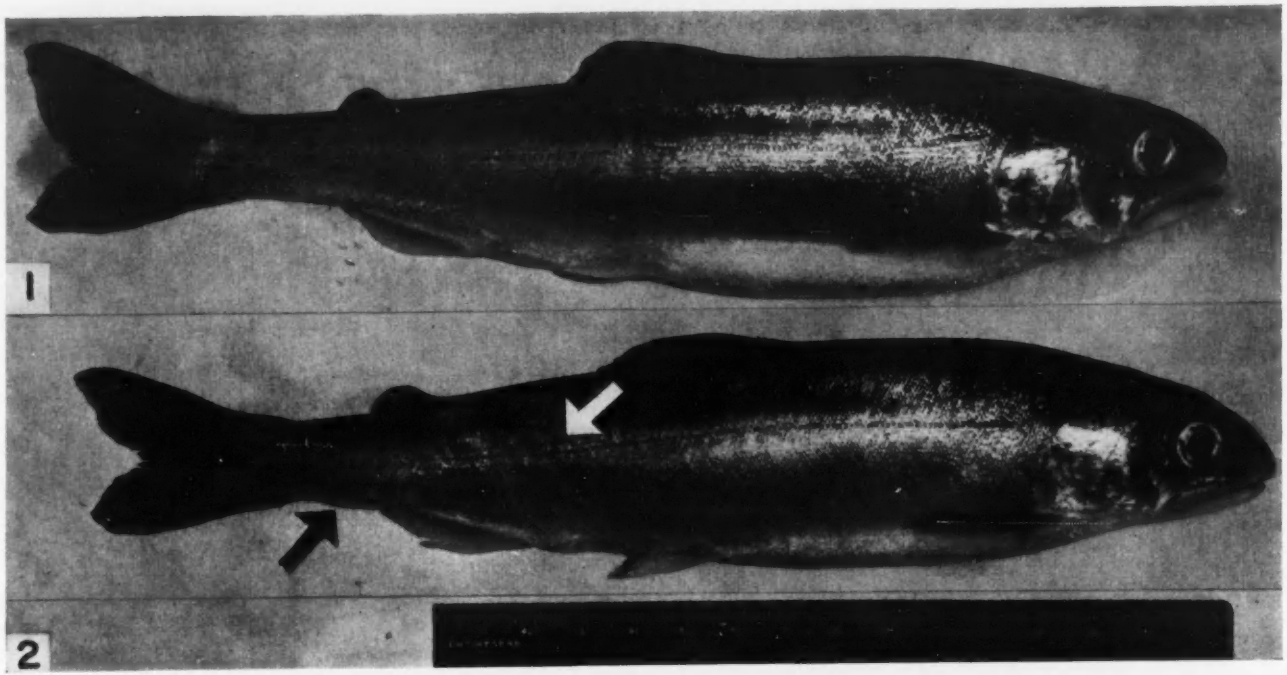

FIG. 1. Healthy, cultured, male pink salmon (*O. gorbuscha*).

FIG. 2. Male pink salmon from same culture but probably infected with kidney disease. The dark arrow indicates a subcutaneous swelling which contained milky fluid filled with cellular debris and typical Gram-positive diplobacilli. This type of swelling was not common but was one of the few visible, external symptoms. The light arrow shows a small blister, more frequently appearing on infected fish than the swelling.

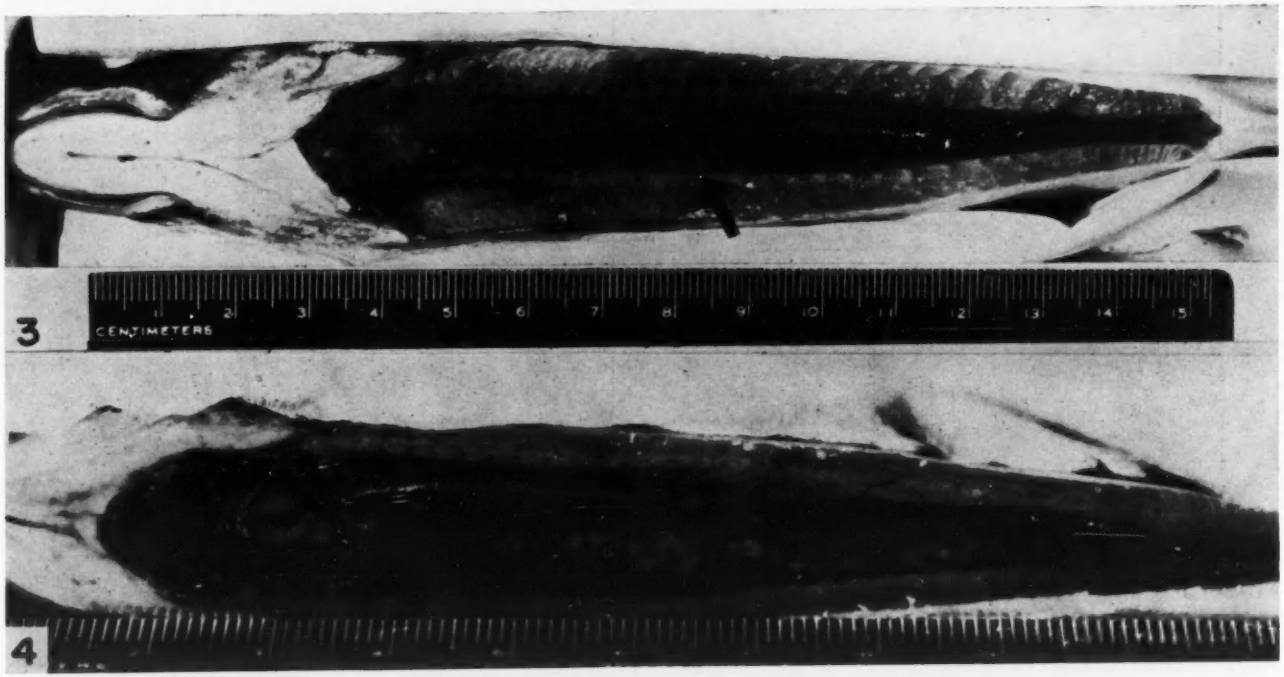

FIG. 3. Healthy, cultured, male pink salmon with kidney exposed. The arrow shows a corpuscle of Stannius.

FIG. 4. Diseased, male pink salmon from same culture; kidney exposed to show typical kidney disease lesions which contained masses of Gram-positive diplobacilli.

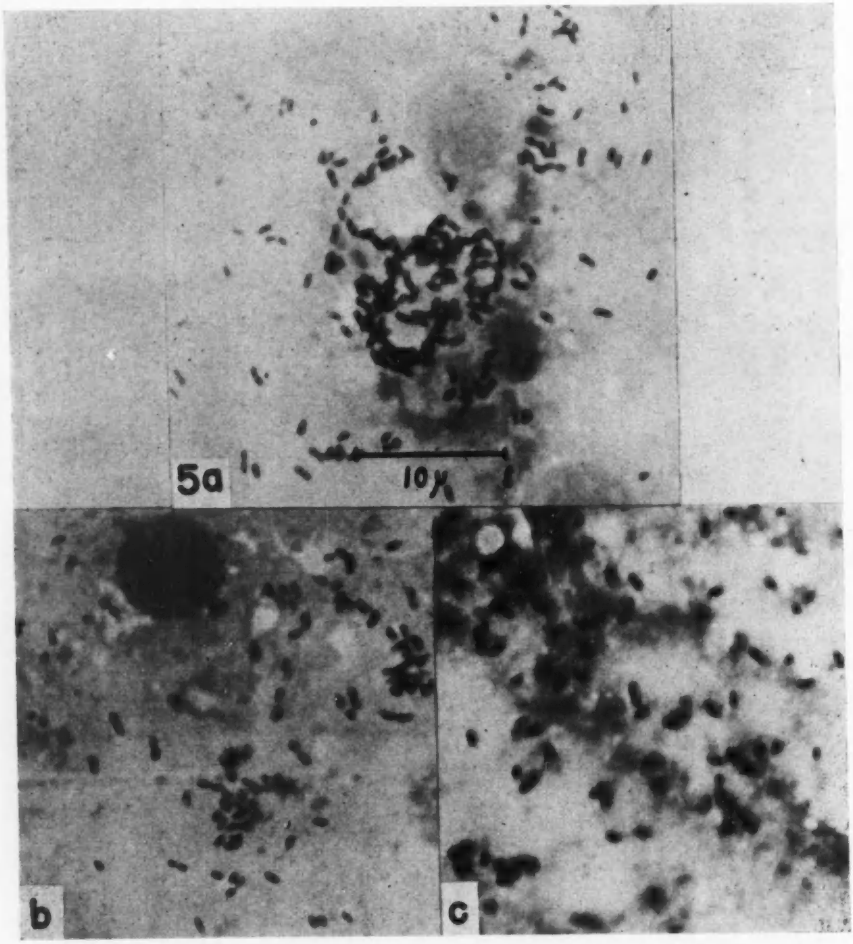

FIG. 5. Gram stains of cells taken from kidney lesions of three diseased pink salmon. Various morphological types are seen in the three fields, a, b and c.

The Annual Oceanographic Cycle at Igloolik in the Canadian Arctic II. The Phytoplankton[1]

"Calanus" Series, No. 17

By Adam S. Bursa

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ABSTRACT

Phytoplankton populations near Igloolik, northern Foxe Basin, began to increase in late April, and reached their climax in mid-August. The rapid late-August decline of the phytoplankton populations coincided with diminishing light. Diatoms were the main biomass producers in Igloolik and the principal food for the marine fauna. The succession of spring Pennatae and summer Centriceae apparently was caused by light and ice conditions. Taxonomic composition of the Igloolik phytoplankton was influenced by the fast ice and by the shallowness and hydrographic uniformity of the adjacent areas. Descriptions are given of two new species of dinoflagellates, *Gyrodinium arcticum* and *Gymnodinium intercalaris*, and the new coccolithine flagellate *Pontosphaera ditrematolitha*.

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INTRODUCTION

IGLOOLIK ISLAND has been visited only on rare occasions by arctic expeditions. The *Calanus* expedition occupied a collection station near Igloolik from September 1955 to September 1956 (Fig. 1). The continuity of the hydrographic observa-

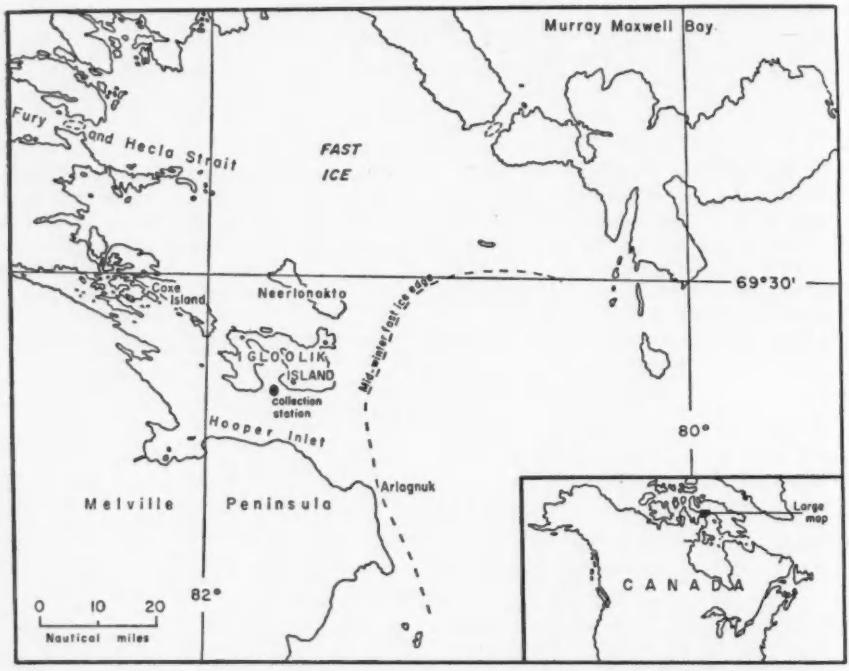

FIG. 1. Northwestern Foxe Basin and the eastern end of Fury and Hecla Strait. The area represented on the large map is shown in the inset.

tions and plankton collections, taken about twice a month, makes this material especially valuable from the oceanographic point of view. Details of sampling procedure have already been described in part I of this series which deals with the zooplankton and physical and chemical data (Grainger, 1959).

METHODS

Quantitative phytoplankton samples collected with a Nansen water-bottle were stored in 170-ml glass bottles with plastic tops, and were later examined with the Utermöhl inverted microscope. Quantitative phytoplankton estimates were made on 25-, 10-, and 5-ml samples after sedimentation in cylinders. Rare organisms, and those difficult to identify, were transferred with a pipette to the

objective glass, then studied under the required magnification with a compound microscope with front phase illumination. It was sometimes convenient, however, to move the dinoflagellates into more suitable positions for identification. This was done by tapping a pencil against the top of the sedimentation cylinder after the quantitative examination of the sample was completed. Both quantitative and vertical net hauls, taken with a net of No. 20 silk, were preserved with neutralized 5% formalin. The efficiency of the taxonomic examination of the vertical net hauls was increased by examination of 1 or 2 cc of net plankton observed later with the inverted microscope. This method seems to be advantageous for studying rare organisms that are often missed when a small number of preparations are studied with the compound microscope. Lugol solutions and methylene blue were used for staining membranes and starch. Javel water was applied for examination of the membrane plates in dinoflagellates. The numerical estimations of plankton were made with objectives 10×, 25×, and 40×. Oculars of 6×, 8×, and 12× were used according to the size of the organisms under examination.

GENERAL HYDROGRAPHICAL AND ECOLOGICAL FEATURES OF IGLOOLIK

All data on ice, light, temperature, oxygen and phosphates discussed here were obtained from Grainger (1959). Emphasis here will be placed on the biological aspects of the phytoplankton and the relation of the phytoplankton to hydrographical conditions.

Light

Light is a limiting factor for photosynthesis of plankton in arctic, ice-bound regions. Submarine light measurements were not made at Igloolik; however, the duration of the screening effect of ice upon light penetration of the water, lasting from late November until mid-January, is shown in Fig. 2. During this period direct light was completely absent. Direct light lasting 24 hours per day extended from mid-May until the end of July, with nearly equal periods of direct light and darkness occurring in early October and in early March.

Temperature

Temperature and salinity in northern seas are never limiting factors for plankton as a whole, only for some species (Steemann-Nielsen, 1935). According to Steemann-Nielsen and Hansen (1959), "in the arctic the influence of the low temperature on the rate of photosynthesis is counteracted by a higher concentration of enzymes". The temperature extremes at Igloolik were very narrow (Fig. 2b), between +1.72°C and −1.80°C. The maximum water temperature occurred at the beginning of September, at a time of decline of phytoplankton. The 7-month period of subzero temperature (November-May) was a stagnant one for plants, but one of significant reproductive activity for part of the zooplankton. The first slight increase of phytoplankton populations took place

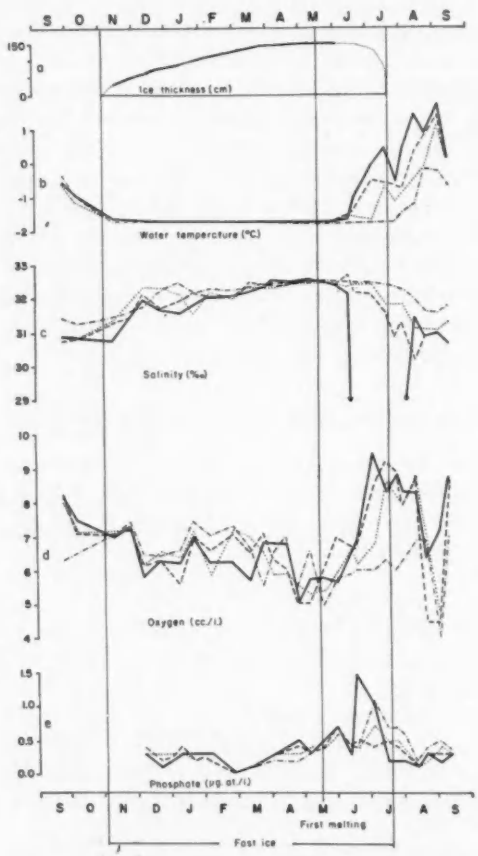

FIG. 2. The annual cycles of (a) ice thickness, (b) water temperature, (c) salinity, (d) dissolved oxygen, and (e) dissolved inorganic phosphate, from September 1955 until September 1956.

Depths are indicated as follows: *surface*, full line; *10m*, broken line; *25m*, dotted line; *50m*, dots and dashes.

after winter when a small rise of temperature (0.5°C) in May was noticed. According to Braarud (1945) small temperature changes in *Chaetoceros* induce microspore formation. Supposedly a similar effect is induced during temperature changes in plankton.

ICE

In the Igloolik area ice thickness increased from November until early May, when it reached 152 cm. Melting began in early May, and continued until mid-July (Fig. 2a).

Ice affects salinity, temperature, light penetration and plankton present in arctic waters. Gran (1904, 1908) found 84 diatom species in the arctic ice previously originated in various ecological niches. The true planktonic forms were more common than freshwater and brackish species. The surface of the arctic ice, melting ponds on the ice, and the under surface of the ice are inhabited by diatoms and flagellates. The flora of these ecological niches varies according to the origin of the ice and its locality. It includes benthic, planktonic, estuarine and freshwater organisms frozen during ice formation.

Regularly stratified ice structure, as observed by the author, was common around Baffin Island in 1956. It developed supposedly in inshore waters, in non-turbulent areas where phytoplankton is abundant. The amorphous, old ice contained benthic organisms when freezing of turbulent water areas took place. As observed by the author during the expedition of the *Labrador* to Foxe Basin in 1956, brown-green layers alternating with colourless ice were formed by trapped plankton diatoms. A piece of ice taken in Lancaster Sound (1956) was melted by the author. Many diatoms became motile again but a great many were plasmolized or dead. Since enormous populations of diatoms are trapped in the arctic ice, ice melting favours their return to the plankton, mostly in June and July. The markedly stratified structure of ice supposedly develops when diatom populations accumulate under the ice surface when freezing takes place. The wider green layers of ice may form when diatoms are numerous and water is calm in late August and September when freezing starts.

A diatom film, collected by the Atlantic Oceanographic Group on March 27, 1957 in the Gulf of St. Lawrence and examined by the author contained 32 species, mostly of planktonic origin. Since they were taken in March and represented large populations it is thought that they had begun to grow early in winter darkness (unpublished data).

The dirty yellow ice of Foxe Basin, typical for this area, shows no special structure, according to Campbell and Collin (1958). It is usually old pack ice which has lost its structure while freezing and refreezing. Four to 8 million tons of ice sediment are formed annually in Foxe Basin, as estimated by Campbell and Collin (1958). During the ice-melting period all nutrients contained in the ice enter the water, stimulating plankton metabolism. Observations by Dr A.W. Mansfield (personal communication) indicate that a prevalent north wind

accelerates the speed of the ice floes carried out from Fury and Hecla Strait. It largely clears the ice from northwest Foxe Basin, as happened in 1956. As a result of southeast winds huge ice fields covered the northern part of Foxe Basin in 1957. Since persistent ice delays the maximum of phytoplankton (Braarud and Hope, 1952), the annual production of diatoms in Foxe Basin is evidently affected.

According to Hutchinson (1957) there is only a small effect of ice-melt water upon growth. The influence of the ice-melt waters under arctic conditions is of particular significance from the biological point of view. Recent research on the phytoplankton productivity in Hudson Bay and in northern Foxe Basin (author's unpublished data), show that low salinities during the ice melting period are associated with poor phytoplankton populations, which increase with higher salinities found in the deeper water layers. In Igloolik the immediate surface layer harboured initial populations of diatoms at a time when no melting had occurred; with a decrease of salinity, plankton populations simultaneously decreased from late May until mid-June, by which time diatom populations were markedly reduced. The gradual increase of the surface populations coincided with rising salinities (Fig. 3) observed between July and September. If occasionally larger diatom populations were found at the surface with low salinity they were presumably brought up from the lower depth where production of phytoplankton was always higher.

Salinity

Salinity as an ecological factor in the marine phytoplankton was studied by Braarud (1951), who reported variation in the rate of reproduction with varying salinities in Coccolithineae, Cryptomonadineae and Dinoflagellatae. Though specialized salinity requirements were shown for various arctic diatoms (Grøntved and Seidenfaden, 1938), the ecological characterization of species is still far from being settled. The surface phytoplankton is exposed to greater salinity changes than deeper water layers. Microstratigraphy of the surface salinities at Rowley Island (Foxe Basin) made during the *Calanus* expedition of 1957 shows that great salinity changes take place only within 0–2 metres of the surface.

At Igloolik, salinity values varied between 30.70‰ and 31.50‰ at all depths from September 25 until November 10 (Fig. 2c). In early December they rose at all depths, to 32.03‰ at the surface, to 32.12‰ at 10 m and to 32.36‰ at 25 m, and to 32.48‰ at 50 m in early January. Drops in salinity at all depths began in early February and lasted until early May, when they were everywhere between 32.48‰ and 32.59‰. Salinity changes in the deeper layers were slow and presumably did not affect phytoplankton metabolism. Coincident with the first indication of spring melting, the salinity at the surface fell slowly from May 5 until June 13, then rapidly to 27.01‰ on June 19, to 1.68‰ on July 2, and to less than 1.68‰ on July 15. It rose again to 10.41‰ on July 25, to 19.94‰ on August 1, and to 31.56‰ on August 11.

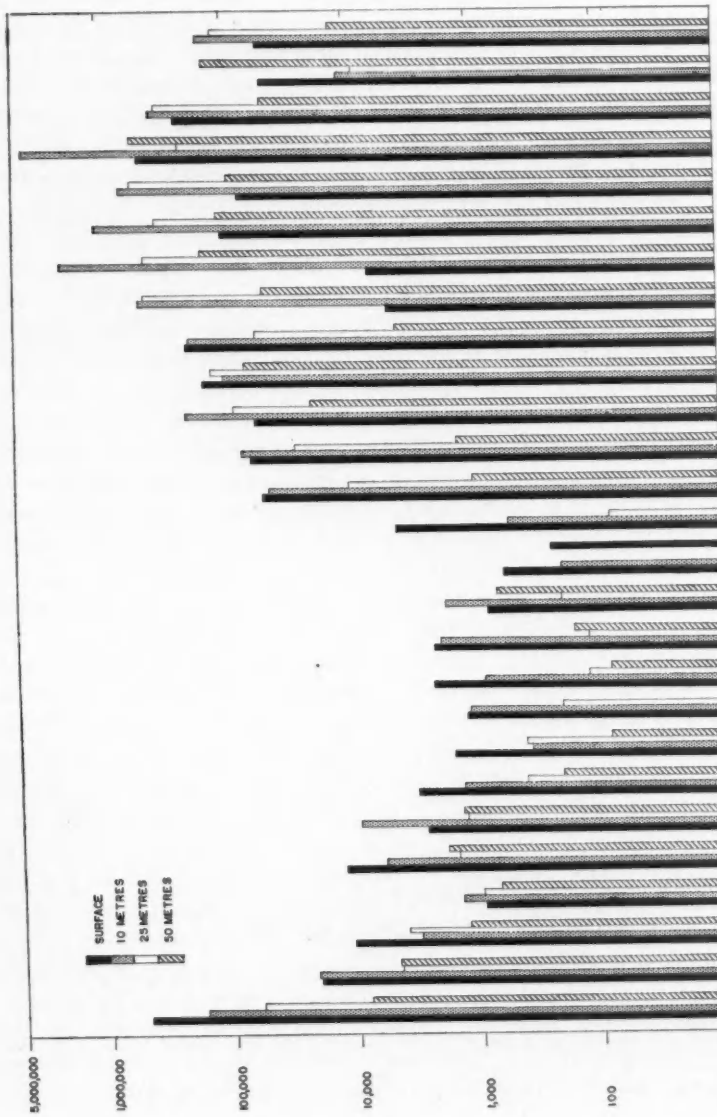

FIG. 3. Histogram showing quantitative features of phytoplankton populations of Igloolik during the entire year at four depths. Counts are given as cells per litre on the logarithmic scale on the left.

Oxygen

Oxygen distribution at Igloolik is illustrated by Fig. 2d. Oxygen saturation values increased from relatively low values on January 9 to 81.55% at the surface, 82.5% at 10 m, 83.6% at 25 m and 86.5% at 50 m on January 23. This increase could probably be related to introduction of new water masses from the open water area newly illuminated by the sun at that time. Decrease of oxygen took place again on February 7. Increase on February 27 was found not at the surface but at 10 and 50 m. Minor oxygen fluctuations occurred from this time until the end of May, although the size of the diatom population appeared to be sufficient to produce higher oxygen content if light conditions had been more favourable. Dim light under the ice continued until June 19, when a low oxygen level was found in spite of large populations of diatoms. The situation changed on July 2 when supersaturation occurred at 10 m and oxygen saturation percentage reached 102.3%. This could be related to the great phytoplankton populations counted at that depth. The very poor populations at the surface and the relatively high oxygen content of 91.0% were presumably caused by vertical mixing. Further vertical extension of the supersaturated oxygen layer was noticed on July 15, when oxygen reached its highest supersaturation value, 110.3% at the surface and 103.7% at 25 m. Although further increase of phytoplankton populations took place on July 25, there was a slight decline in the oxygen content. This was a time when pennate diatoms were still common but were forming cysts. A rise in saturation values took place from the surface to 25 m on August 11, when the climax of the annual production was reached, with the occurrence of the intensively metabolizing Centriceae. Rapid decline in oxygen production on August 20, in spite of large diatom populations, is basically explained by the approaching end of the season and the mass production of resting spores. This decline occurred particularly in the water layer from 10 to 50 m, where the oxygen content was reduced from 55.9 to 49.4%. Some changes occurred on September 13, associated with the replacement of water masses richer in phytoplankton than those observed on September 2, and these may be responsible for the rise in oxygen values to supersaturation at the surface and 10 m, and for the subsaturation at 50 m. Probably new water masses containing still greater diatom populations and higher oxygen content entered the collection station.

Since the general form of the oxygen curve is in fact built up from the oxygen cycles of many plankton organisms, the succession of species and physiological activity in this period of the season could be of value for oxygen interpretation. Since I have observed that great diatom populations are often associated with low oxygen values because of reduced photosynthesis during resting spore formation, a list of species is given, showing: (a) a group of species producing resting spores and auxospores; and (b) species in which formation of the resting spores are not observed. (Tables I and II).

TABLE I. Species of diatoms in which formation of resting spores was observed.

Melosira arctica	*Chaetoceros laciniosus*
M. islandica	*Ch. wighami*
Melosira sp.	*Ch. curvisetus*
Thalassiosira nordenskjöldi	*Ch. debilis*
Th. gravida	*Ch. socialis*
Th. rotula	*Ch. gracilis*
Coscinodiscus grani	*Chaetoceros* sp.
Coscinodiscus sp.	*Biddulphia aurita*
Coscinodiscus oculis iridis	*Fragillaria cylindrus*
Rhizosolenia styliformis	*Navicula grani*
Rh. alata	*N. septentrionalis*
Chaetoceros teres	*Achnantes taeniata*
Ch. lorenzianus	*Lauderia glacialis*
Ch. compressus	*Denotula confervacea*
Ch. constrictus	*Synedra* sp.
Ch. affinis	*Amphiprora hyperborea*

TABLE II. Species of diatoms in which resting spores were not observed.

Coscinosira polychorda	*Bacteriosira fragilis*
Thalassiosira aestivalis	*Navicula* sp.
Th. decipiens	*Gyrosigma spenceri*
Th. subtilis	*Pleurosigma* sp.
Chaetoceros atlanticus	*Nitzschia closterium*
Ch. eibeni	*N. longissima*
Ch. concavicornis	*N. seriata*
Ch. decipiens	*N. pungens*
Ch. perpusillus	*Navicula pelagica*
Eucampia zodiacus	*Thalassiothrix longissima*
Streptotheca thamensis	

It is useful, for general orientation, to compare oxygen data from other arctic and subarctic regions. Oxygen content around the Faeroes and Iceland (Steemann-Nielsen, 1935) rarely shows supersaturation, as at Igloolik. In Denmark Strait higher oxygen values and frequent supersaturation were observed by Braarud (1935). In Allen Bay conditions similar to Igloolik were found (Apollonio, MS, 1956). Oxygen data in Hudson Bay show variable features at many stations. High oxygen content in Hudson Strait (Campbell and Collin, 1958) suggests that conditions for growth of phytoplankton in that area are more advantageous than at Igloolik.

Formation of auxospores was encountered in only 6 planktonic diatoms and was rarely observed. No noticeable effect would be made by such a small population on the total oxygen content. The production of the resting spores found in 34 common diatoms and in three dinoflagellates is obviously more significant and may affect total oxygen content of phytoplankton during resting spore formation (Table I). The resting spores appeared first at the beginning of

spring, increased in mid-season, and reached their peak in August. Factors inducing encystment are different; some dinoflagellates form cysts soon after ingestion of other organisms (Schiller, 1933). Germination of cysts takes place in *Chaetoceros* immediately if conditions are favourable (Braarud, 1945). Encystment in *Goniaulax* species in plankton and in *Gyrodinium californicum* in culture has to be related to salinity-temperature changes (author's unpublished data).

Phosphates

Both light and nutrient supply control metabolic activities of phytoplankton (Brandt, 1899). When nutrients are exhausted phytoplankton growth becomes inhibited in northern waters (Braarud, 1935, Kreps and Verjbinskaya, 1930). Decrease of phytoplankton populations in the antarctic took place before any depletion of nutrients (Hart, 1934). Riley (1946, 1953) shows close correlation between the amount of phytoplankton and nutrients.

The values for inorganic phosphate at Igloolik (Fig. 2e) ranged from 0.1 to 0.4 μg-at/l during December, January and February. The lowest values, close to zero, were found in late February. The maximum occurred in mid-June and values declined in mid-July, and were related to increased populations of diatoms. The highest values of phosphates were noticed when salinity dropped during the ice-melting period.

Stability

The effect of vertical mixing caused by turbulence may be of considerable importance for phytoplankton dynamics (Braarud, 1935; Gran and Braarud, 1935; Riley and Bumpus, 1946). A stable water column generally permits greater phytoplankton growth (Braarud *et al.*, 1953).

At Igloolik, because the maximum depth is only about 50 m, stability seems to have had very little effect, at least upon photosynthesis, since all populations inevitably were suspended within the eutrophic layer. While slight inhibition of photosynthesis may have occurred at the bottom because of slightly reduced light, the entire 50-metre column may for all practical purposes be considered as being within the depth of active photosynthesis.

Horizontal stratification began in May and became gradually more evident during the summer. This had the effect of creating vertical discontinuity in the phytoplankton distribution, resulting in decreased numbers of individuals in the upper layers during the ice-melting period (when the upper layers underwent drastic salinity reductions). Maximum phytoplankton occurrence was between less than 10 and more than 25 m during most of the spring and summer period. Physical changes occurring on September 2, reducing vertical stability, were accompanied by changes in the vertical distribution of the phytoplankton, many of which evidently ceased photosynthetic activity, formed cysts, and sank to the bottom.

SHORT DESCRIPTION OF THE PHYTOPLANKTON CYCLE

The quantitative assessment made with the inverted microscope showed a steady increase of phytoplankton populations starting from late April. After that time the number of species and their populations increased markedly at various depths. The first diatom maximum occurred in mid-July, after which time a considerable decrease was observed. The second peak, associated with the appearance of more species, began in August. The later rapid increase of populations was associated with formation of resting spores in the majority of diatoms. Large populations of diatoms still occurred in September of both 1955 and 1956. The rapid quantitative decline started in October, and the typical winter minimum with its small populations was observed from November until mid-April (Fig. 3).

SEASONAL CHANGES IN PHYTOPLANKTON IN 1955–1956

SEPTEMBER 25[2]

Phytoplankton populations on September 25, 1955 were still numerous as far as total number of species was concerned. There were 23 diatom, 9 dinoflagellate, 4 coccolithophorid and 5 ciliate species recorded. The upper waters showed oxygen close to saturation, 96.8% at the surface, 97.2% at 10 m. Maximum production was found at the surface represented by 491,040 cells per litre. At 10 m there were 168,860 cells per litre, at 25 m 57,520 cells, and at 50 m 6,575 cells. The day before this collection was made weather was calm with the temperature near freezing. The quantitative decline of phytoplankton in September is not only an effect of grazing by zooplankton, probably mainly copepods as shown by Grainger (1959), but also is a result of grazing by ciliates which have their climax after the phytoplankton maximum (Fig. 3). Great oxygen reduction took place during the time of zooplankton maximum. The limited light supply at the surface finally stopped photosynthesis and the majority of species produced resting spores.

OCTOBER 5

Phytoplankton populations in October showed equal numbers of cells at the surface and at 10 m. They still represented a sufficient bulk of food for zooplankton in the entire column of water, although the total number of cells was nearly 20 times smaller in October than in September. *Chaetoceros* species were still represented. *Ch. affinis*, *Ch. curvisetus*, *Ch. wighami*, and *E. zodiacus* exhibited their late maxima of 2,800 cells per litre at the surface, 1,620 at 10 m, and 860 at 25 m. *Fragillaria cylindrus* showed continuous vertical distribution starting from 7,880 cells per litre at the surface, gradually decreasing to 3,260 at 50 m. The smaller number of ciliates showed that both plants and herbivorous forms had reached their final low limit before winter rest.

NOVEMBER 11, 25; DECEMBER 7, 22

The autotrophic plankters were reduced strongly after October 5. The water surface froze and ice reached 33 cm thickness in early November. Five species of *Chaetoceros* formed small populations of a few hundred cells per litre, except for *Ch. compressus*, represented by 1,360 cells per litre at 25 m. Tiny holozoic flagellates were found at all depths in populations varying from 5,600 to 560 per litre. A relatively large number of ciliates (4,260 per litre) and copepods at the surface presumably reduced the phytoplankton to its observed minimum. It is thought that when diatom populations become so reduced that they are insufficient as food, the zooplankton is able to change its diet by devouring various ciliates which are still quite numerous at that time. A further drop in plankton populations took place November 25; 12 species observed under the inverted microscope on that date were represented by only a single or a few individuals. Collections

[2]Copies of tables showing the quantitative occurrence of phytoplankton species on this and the following dates discussed in this section may be obtained from the author.

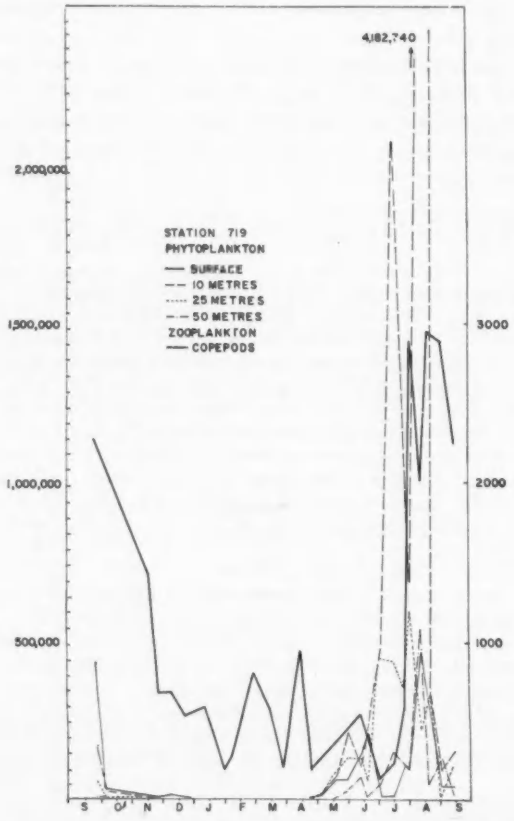

FIG. 4. Phytoplankton populations expressed as number of cells per litre for the four sampled depths, and copepods given as number of individuals per haul.

on December 7 and 22 showed a noticeable increase in diatoms, mainly *Ch. constrictus*, not previously recorded. Presumably this is due to invasion of some allochthonous populations that shifted towards Igloolik. These new populations could be distinguished from the local previously-observed populations by the increased number of *Gymnodinium* sp. and *Warnovia* sp. Observations in December showed further reduction of phytoplankton, especially at the surface and at 10 m. At 25 m there were 17,400 cells per litre of diatoms and flagellated forms. Since the multiplication rate of phytoplankton probably had declined, it is likely that this population was brought in from another area.

JANUARY 9, 23; FEBRUARY 7, 27; MARCH 13, 26

This period showed the typical features of arctic winter. The limiting effects of the ice cover and reduced light supply, associated with low oxygen, drastically reduced the autotrophic plankton to a few individuals per litre. Although poor populations occured in the sedimentation cylinders (4 diatom species), 14 diatom species and 2 flagellates were found in the net. The lowest point in winter production was reached on April 4 and 14, when only 2 specimens of *Nitzschia closterium* and some holozoic flagellates were recorded. The fluctuation of the total phytoplankton population is shown by the following numbers: January 9, 4,000; January 23, 1,720; February 7, 1,360; February 27, 2,680; March 13, 4,340; March 26, 2,340.

APRIL 4, 14 AND 26

The first increase of diatoms was recorded on April 26, close to the surface under the ice. Arctic diatoms characteristic of melting ice, *Achnantes taeniata* and *Fragillaria cylindrus*, were represented by 1,200 and 1,720 cells per litre. Both populations are considered as initial, after winter minimum. There had been little change in temperature and salinity since April 14. It is supposed that decrease in oxygen percentage from April 14 (79.7% at the surface) to April 26 (59.2% at the surface) is related to the under-ice movement of water. Digby (1953) observed the first diatoms under the ice on April 29 in Scoresby Sound, East Greenland. He concluded that these diatoms could have been brought in by water movements from distant open water areas. My opinion is that the diatoms at Igloolik could have originated as an under-ice film, but could be brought from open water areas as well.

Complete absence of phytoplankton occurred only on April 14.

MAY 5, 19 AND 30

Populations of *Achnantes taeniata* and *Fragillaria cylindrus* increased more than 3 times between April 26 and May 5, providing evidence that spring growth of diatoms proceeded in spite of poor light conditions under the ice. Both diatoms occurred as gradually increasing populations and descended into deeper layers. Small populations of *Chaetoceros compressus* and *Ch. curvisetus* appeared. Small unidentified flagellates occurred between the surface and 25 m in numbers close to the number of diatoms. May 19 showed a still more accentuated phase of increasing autotrophic plants, with the dominant *Ach. taeniata* rapidly developing into populations of 47,960 at the surface, 33,800 at 10 m, 22,400 at 25 m and 1,020 at 50 m. During this period the ice began to melt (Fig. 2). This is also reflected in the salinities of May 5: 32.59‰ at the surface, 32.48‰ at 10 m and 32.50‰ at 25 m. Similar features were found on May 19. After May 5 new species appeared: *Denotula confervacea*, an arctic-neritic form with a population of 21,540 cells per litre at 10 m, and the less abundant *Thalassiosira nordenskjøldi* and *Chaetoceros wighami*. The total number of species included 14 diatoms, 2 dinoflagellates and other minor forms. After mid-May the sun remained above the horizon 24 hours of the day. The rapid increase of the diatom population followed progressive heating of the surface and ice-melting. Though salinity at the surface was only slightly different (32.45‰) from that at 10 m (32.41‰), the surface showed 4 times greater production than deeper layers (Fig. 3). Oxygen at the surface had the relatively low value of 66.3%, despite the fairly large populations of diatoms. It increased to 82.4% at 10 m, then decreased at 25 m where larger populations were found. This presumably indicates more stable waters, which favour phytoplankton metabolism. The maximum May production was reached by *Achnantes taeniata* at 10 m with a population of 174,440 cells per litre, and 66,220 at 25 m.

JUNE 13 AND 19

There was a slight decrease in oxygen at 10 m from May 30 to June 13, and a decrease in surface salinity from 32.45‰ to 32.18‰. More intensive melting began in June and areas of rotting ice appeared over the entire fast ice surface. Plankton production was in an advanced phase, as reflected in the great size of populations and the number of species: 16 diatoms were observed in the inverted microscope and 5 additional ones in the net hauls. Among the flagellated species, some *Pontosphera*, *Scyphosphera* and *Lohmannosphera* were found for the first time in the eastern Canadian arctic.

Observations on June 19 show a further drop in salinity to 27.01‰ at the surface, and relatively smaller populations. This probably occurred because of ice-floes covering wide areas for considerable periods of time. Conditions on June 19 at Igloolik show many similarities to observations made by Braarud (1935) in the pack-ice areas of Denmark Strait in respect to phytoplankton composition and water characteristics. However, this similarity is partly accidental, since environmental conditions in the two areas differ considerably. Braarud's (1935) observations are as follows: when the ice was near by, no large volume of plant production was found, oxygen content was low, the concentration of nutrients was almost the same at the surface as at the lower levels, and salinity was nearly the same at all levels. In all four instances given by Braarud the surface had a smaller phytoplankton crop than the 10-metre layer, where the maximum was found. Though no direct quantitative evaluation of ice influence could be made at Igloolik, it is obvious that ice affects greatly both photosynthetic metabolism and growth. Results of Apollonio (1956) at Allen Bay, Cornwallis Island, show some similarity to those found at Igloolik. Further discussion has to be postponed until more data are available.

JULY 2

There was striking decrease in the size of the population at the surface, as compared with June 19, associated with a drop in salinity to 1.68‰. The fast ice had cleared away from Igloolik Island, and by the middle of July the edge had moved into Hooper Inlet, about half way between southeastern Igloolik Island and Turton Bay. Seventeen diatom species were found with the inverted microscope, including the previously absent *Coscinosira polychorda* and *Navicula vanhoffeni* which exhibited their initial phase of growth. *Thalassiosira rotula* and *Streptotheca thamensis* were also observed for the first time. *Chaetoceros decipiens*, *Ch. furcellatus*, *Ch. wighami* and *Fragillaria nana* were found in the net hauls. The surface population became reduced to a few individuals per litre. The great populations of *Achnantes taeniata* (267,000), *Fragillaria cylindrus* and *Fr. islandica* (69,000), *Navicula grani* (53,000), *Thalassiosira nordenskjøldi* (34,000) and other less numerous species indicate that the 10-metre depth showed optimal conditions for diatom growth. However, the dominant *Ach. taeniata* had its maximum at 25 m (403,600 cells per litre) and was still represented by 48,280 cells at 50 m. It was the first time that supersaturation of oxygen at 10 m was reached (102.3%). Although very poor populations were recorded at the surface, oxygen was 91.0% of saturation. Oxygen was thought to be produced by metabolically active diatoms before they sank to the lower depths, where plankton populations were much larger than at the surface. In spite of the fairly large number of diatoms, a decrease of oxygen to 79.8% saturation was observed at 25 m, and furthermore it was 71.1% at 50 m. This was a period of intensive increase of pennate diatoms and the appearance of important biomass producers, among which the genus *Thalassiosira* became more important as the season advanced.

JULY 15 AND 25

This was the period of maximum production of the pennate diatoms, of which *Achnantes taeniata* showed 1,440,000 cells per litre at 10 m. Meanwhile *Chaetoceros wighami* and *Ch. socialis* increased at 10 m to great populations of 146,000 and 72,000 cells per litre. Sixteen species of diatoms were found with the inverted microscope, while in the net samples still more occurred, though in small quantities, including *Chaetoceros karianus*, *Ch. septentrionalis*, *Nitzschia pungens*, *N. frigida*, *Fragillaria nana* and *Lauderia glacialis*. Marked increase of species of *Nitzschia* and *Navicula* and *Melosira islandica* indicates that these forms become a potentially strong component of the phytoplankton. This was still more marked in *Thalassiosira nordenskjøldi* and *Th. rotula*,

represented by 153,400 and 135,000 cells per litre found at 10 m. There was further increase in oxygen percentage at 10 m to 110.3%. At 25 m oxygen still showed supersaturation (103.7%), associated with numerically smaller populations and weaker light conditions. On July 23 the ice edge moved almost to Turton Bay, at whose entrance the collection station was situated (Fig. 1), and by the end of July it was inside the bay. The surface water at that time presumably contained much newly melted ice, and its salinity was low (10.41‰). The brackish forms *Chaetoceros socialis*, *Ch. wighami* and *Nitzschia pungens* became more abundant at that time, being better adapted to the low salinities. The general composition of phytoplankton on July 25 showed gradual decline of pennate diatoms, represented by *Achnantes taeniata* and *Fragillaria cylindrus*. Some Centriceae, such as *Chaetoceros wighami* showed their maxima at 10 m, reaching 461,000 cells per litre. The numerical increase in populations of *Denotula confervacea*, *Nitzschia pungens*, *Melosira islandica* and especially of *Thalassiosira* species, also of flagellated organisms, became more noticeable.

AUGUST 1, 11 AND 20

In early August and September 1956 only small patches of fast ice, along with offshore grounded floes, remained around Igloolik. Only occasional ice floes drifted into Hooper Inlet and Turton Bay. On August 1 the total amount of phytoplankton had decreased only insignificantly at all depths, since the previous observation. The taxonomic composition of the diatoms however was changed by the appearance of new species and decrease in the spring forms. The inverted microscope showed 33 species of flagellated groups and ciliates. The net samples showed another 21 species. This was a period of phytoplankton abundance (Fig. 3). In spite of the large autotrophic populations, oxygen values are below saturation. These probably could be interpreted as a result of cloudy weather conditions. Surface diatom production shows only a slight quantitative increase in spite of a considerable salinity increase. This was probably a result of surface water drift, which can not yet be estimated from our observations. Though the largest diatom populations were found at 10 m, those at 25 m were not much smaller. This indicated continuous vertical distribution of phytoplankton. The 10-metre depth showed fairly large maxima of *Chaetoceros furcellatus* of 122,000 cells per litre, 248,000 *Ch. socialis*, 61,000 *N. seriata* and 56,000 *Th. rotula*. This was a period during which the most important diatoms produced resting spores and ceased their metabolic activities, disappearing from the surface.

The climax of the annual production occurred on August 11. Centriceae predominated over the receding pennate forms. The genus *Chaetoceros* was represented by 7 species among which *Ch. socialis* was most numerous and reached its climax of 3,770,000 cells per litre at 10 m. *Ch. wighami* showed a population of 147,000 cells per litre, and *N. pungens* of 124,800 cells per litre. The increase of surface salinity from 19.94‰ on August 1 to 31.56‰ on August 11 is associated with the increase of *Ch. socialis* to 112,000 cells per litre. Similar increases concerned *Nitzschia pungens*, *Ch. furcellatus* and *Ch. wighami*. Dinoflagellates reached their climax and were represented by 9 species, among which the holozoic *Gymnodinium rubrum* exhibited a maximum of 45,000 cells per litre (Fig. 5, 6). It often ingests various diatoms, dinoflagellates and ciliates, and it is thought to constitute an effective grazing element at the time of its maximum. Various Coccolithineae, previously rare or unnoticed, appeared to be abundant (Fig. 8, 9a-n). The supersaturation extending from the surface to 25 m indicated active photosynthesis, decreasing at 50 m on account of reduced light at that level.

Observations made on August 20 showed an evident decline in the number of species and the number of organisms, resulting from decreased light supply, although the number of species was still relatively high. Physiological rest of autotrophs is suggested by lower oxygen values at the surface and within the lower levels.

Observations made on August 26 show a continuing decline of phytoplankton, which could be effectively grazed by the relatively large populations of ciliates and plankton crustaceans and other animals near their annual maximum, as reported by Grainger (1959). The flagellated organisms were mainly represented by *Pontosphaera huxleyi*, with some other species of Coccolithineae found at all depths (Fig. 8).

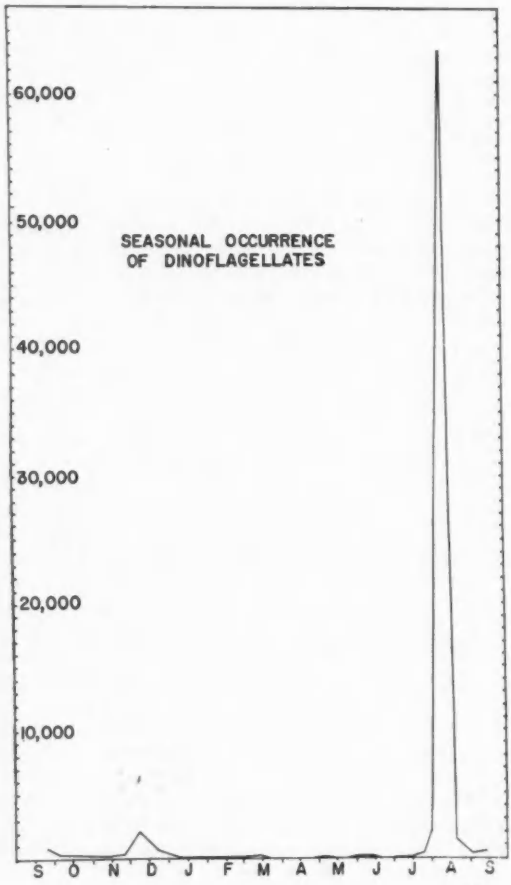

FIG. 5. Seasonal occurrence of dinoflagellates at Igloolik.

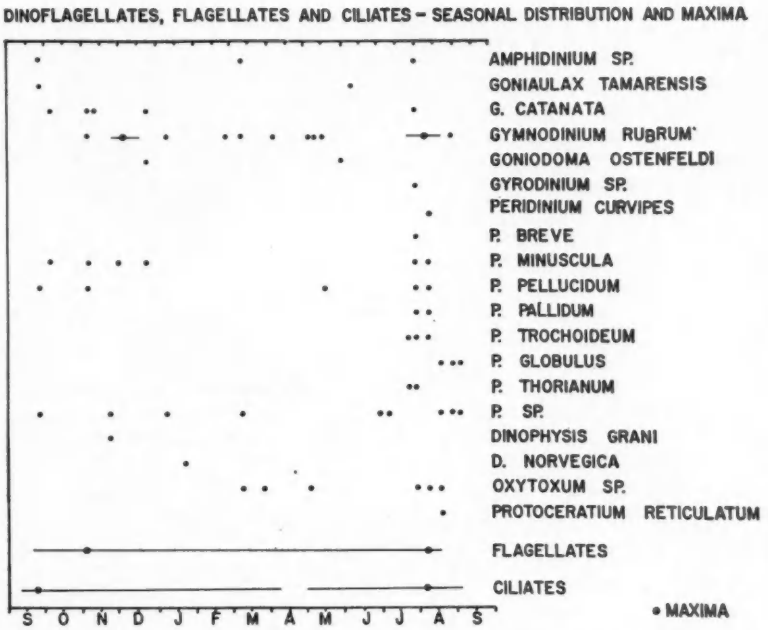

FIG. 6. Seasonal distribution and maxima of dinoflagellates, flagellates and ciliates.

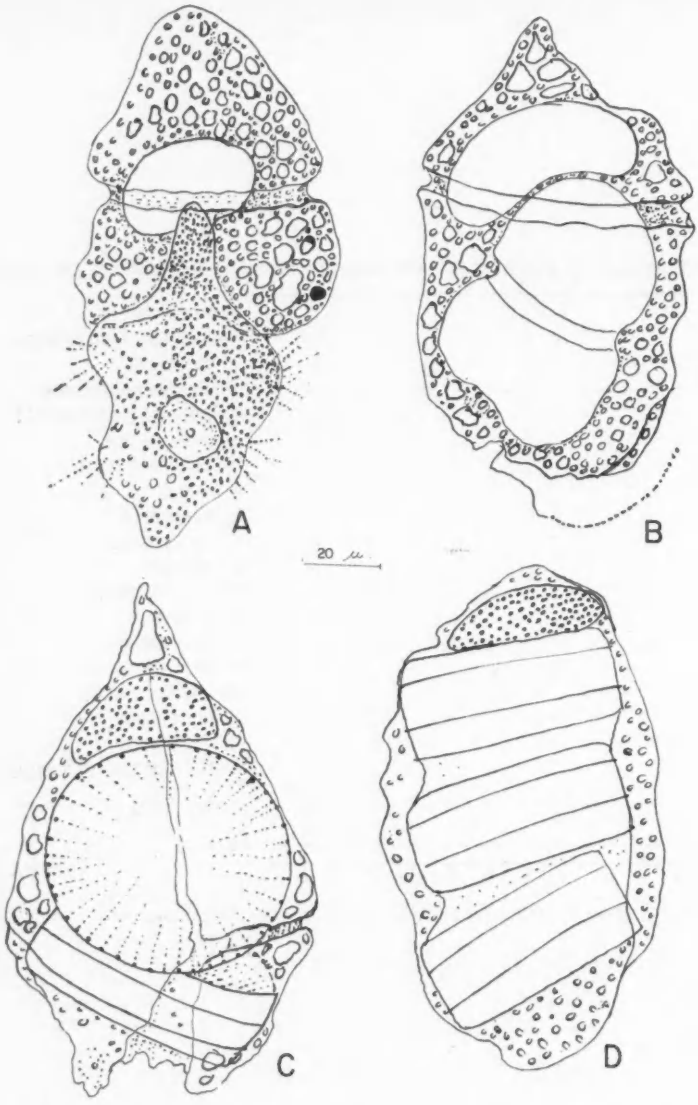

FIG. 7. *Gymnodinium rubrum*. (a) ingesting a ciliate *Strombidium*; (b) containing *Gymnodinium* cell; (c) containing *Thalassiosira rotula*; (d) utterly deformed, containing three cells of *Coscinosira polychorda*, showing nucleus at the apex.

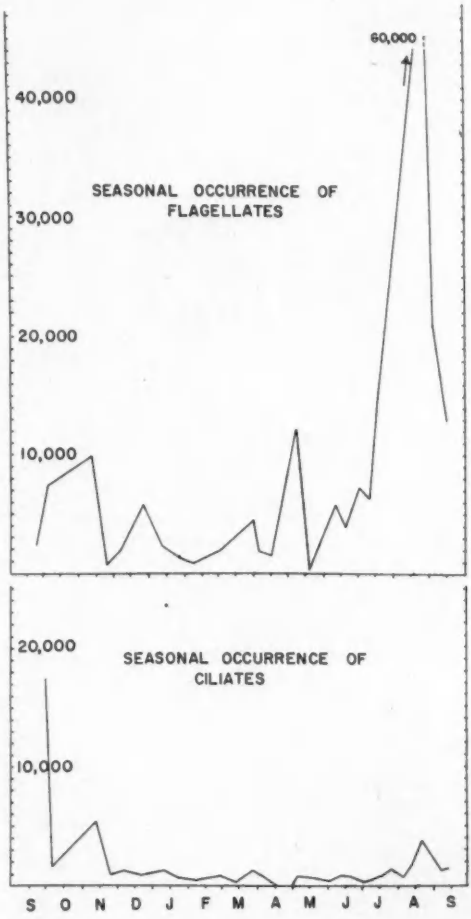

FIG. 8. Seasonal occurrence of flagellates (top), and of ciliates (bottom).

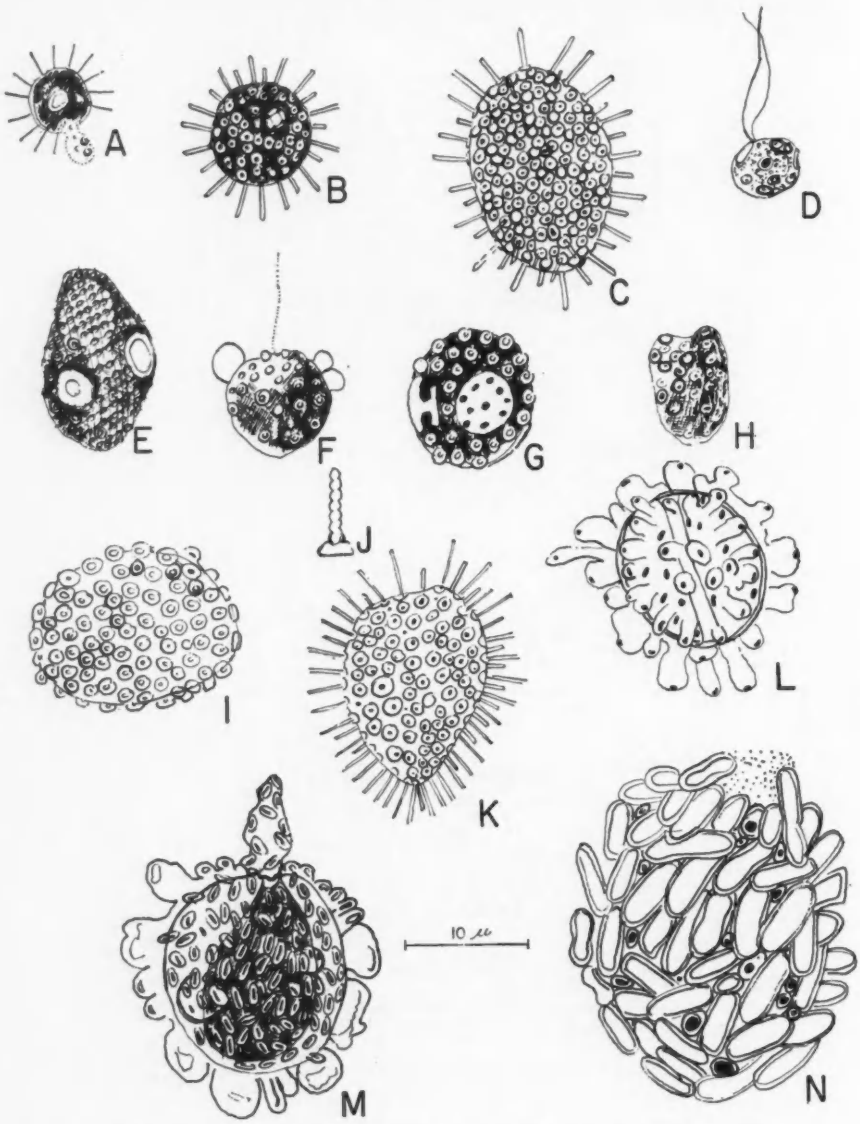

FIG. 9. *Pontosphaera nigra* (a-c), *Pontosphaera huxleyi* (d), *Pontosphaera ditrematolitha* (e-g), *Syracosphaera* sp. (h), *Pontosphaera* sp. (i), *Scyphosphaera* sp. (k), a single coccolith (j), *Lohmannosphaera* sp. (l, m), *Coccolithus pelagicus* (n).

SEPTEMBER 2 AND 13

Autotrophic organisms were represented by 18 species, a great reduction since the late August observation. There seemed to be a definite cessation in metabolic activities except for formation of resting spores, which was quite commonly observed. Vertical oxygen distribution shows subsaturation; the highest value was 93.3%, at the surface, decreasing rapidly to 55.9% at 10 m and 58.3% at 25 m. The water layer at 50 m showed a still lower oxygen content, 49.4% though a relatively large population of over half a million diatoms was found in it.

Observations on September 13 showed an increase of oxygen saturation to 105.2% at the surface and 102.7% at 10 m, while at 25 and 50 m 96.2% and 83.8% were recorded. Presumably new water masses with larger phytoplankton populations replaced the local phytoplankton of September 2. It is not possible, however, to explain this irregularity with certainty, because no data from adjacent areas were taken simultaneously.

VERTICAL DISTRIBUTION OF PHYTOPLANKTON

The vertical distribution of phytoplankton has to be related to various factors such as shape of cells, presence of bristles, and oil or gaseous vacuoles (Gran, 1912; Allen, 1932). Oily discharges from *Coscinodiscus* occurred at the surface of the North Sea (Grøntved, 1952). Experiments were made by the author on preserved *Coscinodiscus* plankton samples. These diatoms which contained large drops of oil gathered in large numbers at the surface of the sedimentation cylinders, while those in which oil was not yet developed covered the bottom of the cylinder. There was also a number of cells suspended in the middle of the cylinder. The floating capacity of diatoms appears to be associated also with the frequency of cell division (Gross and Zeuthen, 1948). Small phytoplankters are better adapted for flotation than are the larger forms (Munk and Riley, 1952). Sinking of phytoplankton in the sea does not necessarily occur in sheltered or calm waters (Grøntved and Steemann-Nielsen, 1957). Igloolik observations indicate that the sinking of diatoms took place when the largest standing crop of plankters was observed to contain resting spores, with membranes of greater specific weight than protoplasm.

Total estimates of the annual mean standing crop at the four depths show striking differences in size of populations (Table III).

TABLE III. Mean annual standing crop of phytoplankton at Igloolik, in number of cells per litre.

Surface	71,038
10 *m*	357,464
25 *m*	101,453
50 *m*	45,043

The surface water, in spite of the high solar illumination, harbours small populations which are exposed to drastic salinity fluctuations. These reach their

lowest values during the ice melting period. The Fisheries Research Board of Canada's *Calanus* expedition in 1957 at Rowley Island showed that brackish water of the lowest salinities formed a layer 2 m deep (unpublished data). Such conditions create a real osmotic barrier for euryhaline plankters from higher salinities below. The maximum phytoplankton production was confined to the 10-metre depth. It was 5 times greater than the production at the remaining depths. The high oxygen values found at 10 m and below in Hebron Fjord in Labrador (Nutt and Coachman, 1956) and those of Igloolik allow one to conclude that the largest autotrophic populations of diatoms generally are found between approximately 5 and 19 m. The mean annual standing crop in Igloolik at 25 m is nearly equal to that at the surface. The mean annual standing crop at 50 m, in spite of the low amount of solar energy, is not much less than the surface crop. This depth in arctic latitudes is usually considered as non-productive, and plankton populations found in it probably do not originate *in situ* but have sunk down from the surface layers.

QUANTITATIVE RELATIONSHIPS

Main Taxonomic Groups

Quantitative relationships among the main taxonomic groups: diatoms, dinoflagellates and ciliates, are shown in Fig. 10. The totals for each group were obtained by adding all plankters of the surface, 10-, 25- and 50-metre samples taken at Igloolik during the 28 station occupations. The largest block of phytoplankton organisms is represented by diatoms, for which the average density was 150,000 cells per litre in the 112 litres of water sampled during the entire season of observation. The main block of the column is divided into a left section representing Centriceae, which produced twice as large an "annual crop" as Pennatae, shown on the right side. The extreme quantitative disproportion is apparent when the total of all flagellates, averaging 2,200 cells per litre, is compared with the large number of diatoms. Although dinoflagellates were represented by 32 species, their total "annual crop" was relatively small, averaging 660 individuals per litre. Because the majority of dinoflagellates found in Igloolik were holozoic and only a small fraction were autotrophic most of them may represent grazers, while a small number only are real autotrophic producers of biomass. The smallest block of ciliates, with an average population of 240 individuals per litre, represents real grazers which are of unknown significance in the food chain of plankton. The reader may evaluate briefly the total participation of each group concerned by comparing their "annual standing crops" (Fig. 10).

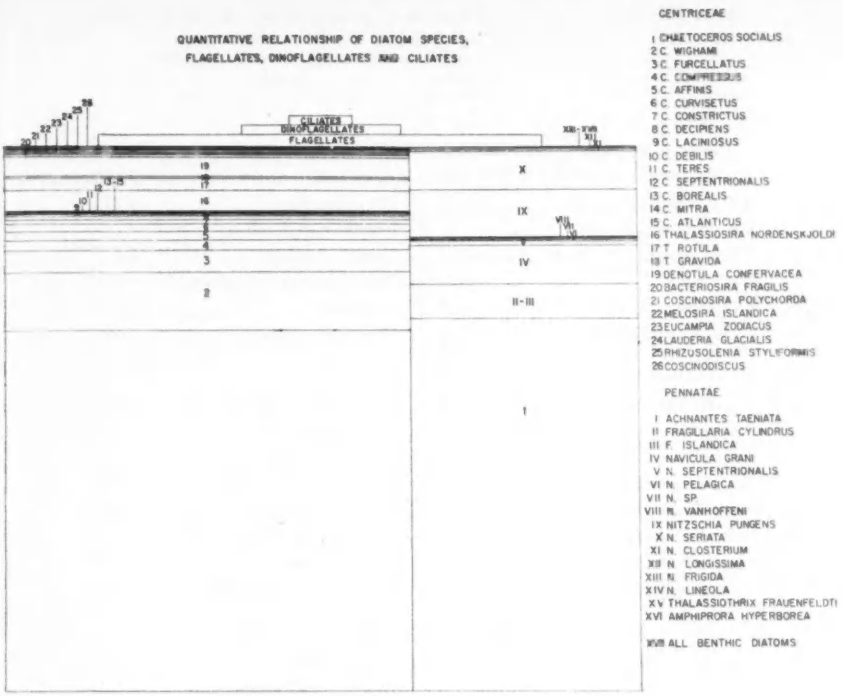

FIG. 10. Quantitative relationship of diatoms, flagellates, dinoflagellates and ciliates. Explanation in text.

ABUNDANCE OF THE VARIOUS SPECIES

The total number of individuals of each species was arranged into 3 groups called major, intermediate and minor, according to frequency of occurrence in the collections. The major group consists of 16 species which are the main biomass producers (Table IVa). The typical arctic diatom element was mainly represented in this group.

The intermediate group consists of 16 species of mixed ecological origin, mostly cosmopolitan and arctic (Table IVb).

The minor group has been divided into those found in the inverted microscope (Table IVc) and those which occurred only in the net hauls (Table IVd). This is in fact the group with the greatest number of species, including 39 diatoms, 30 dinoflagellates, 4 flagellates and 6 Coccolithineae. This group is considered a potential seeding stock, and under favourable conditions may increase in size, thus becoming significant food for zooplankton.

TABLE IV. Major, intermediate and minor groups of phytoplankton species, with their average numbers in cells per litre.

Species	Number	Species	Number
A. MAJOR GROUP			
Chaetoceros socialis	62,685	*Nitzschia pungens*	4,611
Ch. wighami	10,269	*N. seriata*	3,640
Ch. furcellatus	3,778	*Navicula grani*	3,758
Ch. compressus	1,749	*Fragillaria islandica*	
Ch. subsecundus	1,563	and *cylindrus*	3,313
Ch. affinis	1,514	*Thalassiosira nordenskjøldi*	3,514
Ch. decipiens	667	*Th. rotula*	2,092
Achnantes taeniata	36,432	*Denotula confervacea*	3,316
B. INTERMEDIATE GROUP			
Chaetoceros laciniosus	394	*N. septentrionalis*	395
Ch. debilis	162	*Navicula* sp.	78
Ch. teres	154	*Lauderia glacialis*	192
Ch. septentrionalis	153	*Coscinosira polychorda*	286
Bacteriosira fragilis	303	*Eucampia zodiacus*	264
Melosira islandica	285	*Nitzschia closterium*	193
Navicula pelagica	209	*N. longissima*	190
N. vanhoffeni	0.36	*Rhizosolenia styliformis*	96
C. MINOR GROUP, FOUND IN THE INVERTED MICROSCOPE			
Chaetoceros borealis	36	*Coscinodiscus* sp.	11
Chaetoceros atlanticus		*Amphiprora hyperborea*	4
and *Ch. mitra*	6	All benthic diatoms	29
Nitzschia frigida	28	*Thalassiothrix frauenfeldi*	8
N. lineola	23		
D. MINOR GROUP, FOUND ONLY IN THE NET SAMPLES			
Chaetoceros eibeni, Ch. gracilis, Ch. perpusillus, Ch. karianus, Melosira arenaria, M. borreri, Synedra sp., *Coscinodiscus excentricus, Coscinodiscus* sp., *Fragillaria* sp., *Pleurosigma* sp., *Pinnularia* sp., *Navicula* sp., *Gyrosigma spenceri, Gyrosigma* sp., *Nitzschia bilobata, Strepthotheca thamensis, Thalassiosira subtilis, Th. condensata, Thalassiosira* sp., *Cocconeis placentula, Cocconeis* sp.			

SOME DYNAMIC FEATURES OF MORE COMMON DIATOM POPULATIONS

Thirteen diatom species were chosen in order to show quantitative fluctuations of their populations in the plankton (Fig. 11–13). Some diatoms, like *Thalassiosira gravida, Th. nordenskjøldi, Melosira islandica* and *Chaetoceros furcellatus* develop only a single maximum during a vegetative season, this cycle being called unimodal. Species like *Chaetoceros wighami, Ch. constrictus* and *Thalassiosira rotula* are called bimodal, since two separate maxima are formed by their populations. The polymodal species show three or more even or uneven maxima.

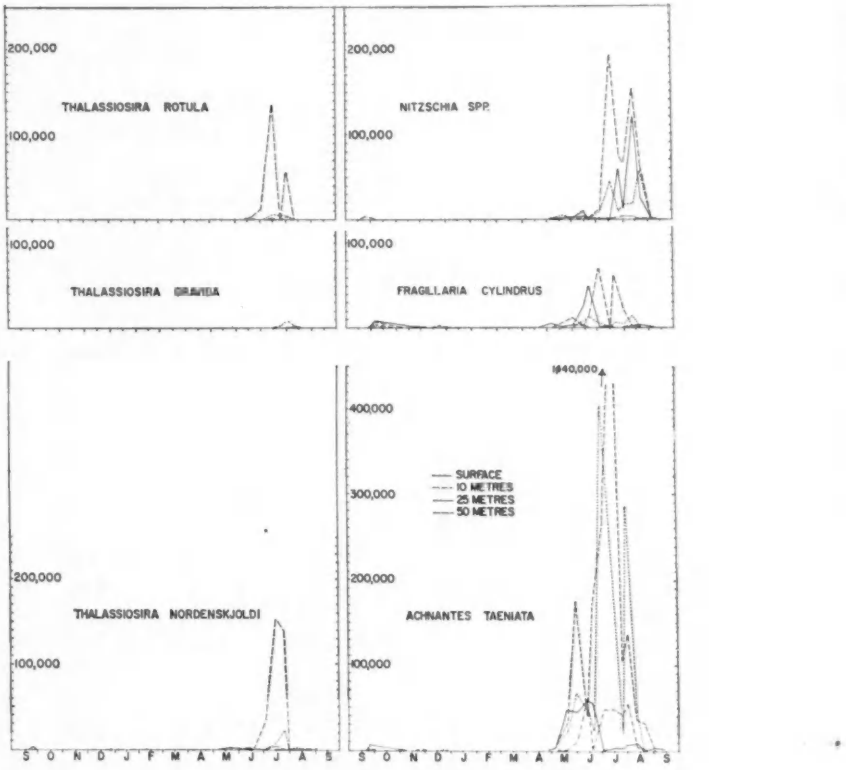

FIG. 11. Quantitative dynamics of the more common diatoms and their annual cycles.

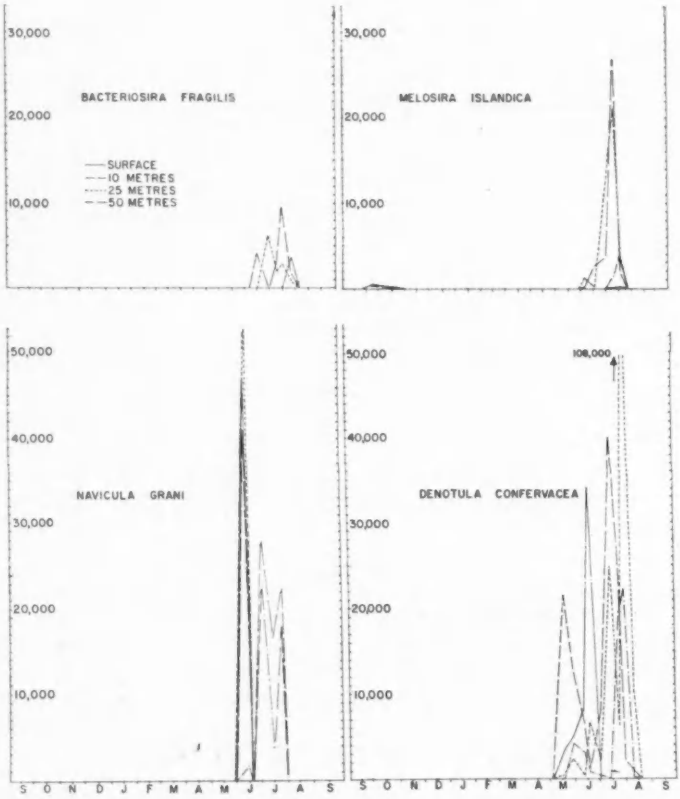

FIG. 12. Quantitative dynamics of the more common diatoms and their annual cycles.

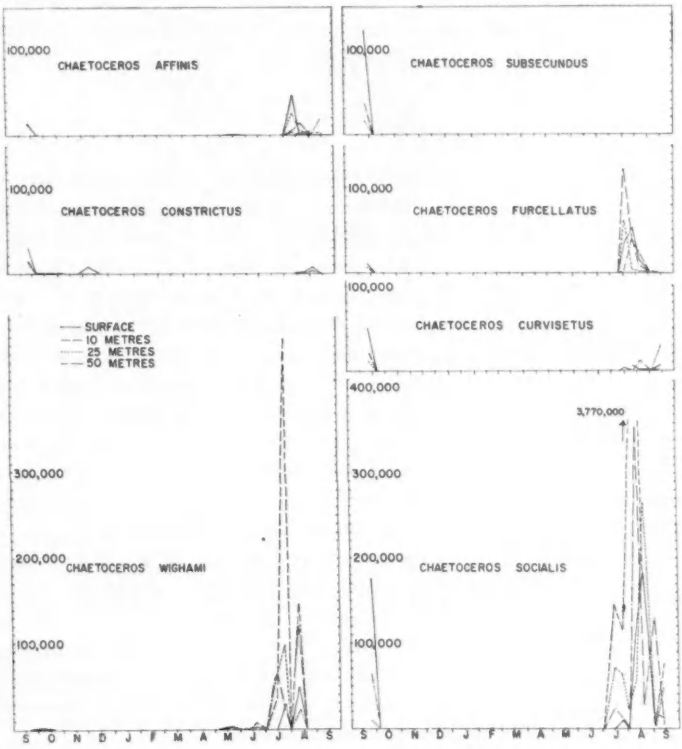

FIG. 13. Quantitative dynamics of the more common diatoms and their annual cycles.

In this group belong *Bacteriosira fragilis*, *Navicula grani*, *Denotula confervacea*, *Fragillaria cylindrus* and *Achnantes taeniata*. Taxonomic identification of diatoms was made using the monographs of Hustedt (1930) and Cupp (1943).

The nature of the quantitative fluctuations in plankton is unexplained. It is supposed that the unimodal type of cycle develops in species where populations are physiologically uniform and show similar features in growth and reproduction. Species exhibiting polymodal curves may consist of physiologically heterogeneous populations, probably differentiated into various physiological groups, which alternate in the sea in sequence with the seasons.

DINOFLAGELLATES

Thirty-two species of dinoflagellates found in Igloolik samples were common only in August and September. The occurrence of most of them in the net hauls was usually restricted to single individuals only, or they were absent from the inverted microscope chambers. To increase the chance of finding rare forms of dinoflagellates, 1 or 2 ml of the plankton sediment were taken with a calibrated pipette and examined with the inverted microscope after filling the sedimentation chambers with water. Such a procedure increases the possibility of finding rare organisms by about 150 to 300 times over the use of single ordinary compound microscope preparations. The time-consuming identifications usually make it possible to examine only a few preparations, so the chance of finding rare species with the inverted microscope are very much better than with the ordinary compound microscope. Works by Schiller (1933, 1937), Paulsen (1908, 1949), and Wood (1954) were used for identification of dinoflagellates.

The thecate forms of dinoflagellates were represented by 19 species, forming small populations seldom exceeding 300 cells per litre. Although the athecate forms were represented by 6 species only, the yearly total of cells collected averaged more than 450 cells per litre. The total number of dinoflagellates taken at Igloolik averaged 665 individuals per litre. The largest populations were 45,000 cells per litre at the surface and 17,670 at 10 m, observed on 11 August, consisting mainly of *Gymnodinium rubrum*.

Some Igloolik dinoflagellates were efficient grazers. Among them *G. rubrum* was able to ingest diatoms (*Thalassiosira*, *Coscinosira*), dinoflagellates and protozoans larger than itself (Fig. 7, a-d). Holozoic nutrition was observed on a few occasions in *Peridinium globulus* (Fig. 14). The cosmopolitan group was dominant, while typical arctic species were less abundant. *Peridinium grani*, *P. quarnerense*, *P. pallidum*, *P. pellucidum*, and *P. minuscula* were more common than *P. roseum*, *P. groenlandicum*, *P. thorianum*, *P. breve*, *P. curvipes*, *Dinophysis grani*, *D. norvegica*, *Goniodoma* sp., *Goniaulax tamarensis* and *G. catenata*.

The preponderance of holozoic over autotrophic dinoflagellates in the Igloolik area is interpreted as a common phenomenon in the arctic biotope, where a natural selection is imposed by the long period of darkness and low temperature. Holozoic

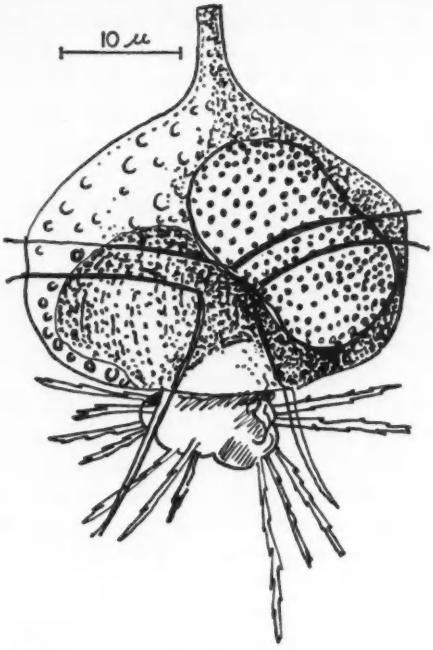

FIG. 14. *Peridinium globulus* ingesting an unidentified flagellate.

plankters appear to be less affected by both these factors, obtaining their energy requirements by phagocytosis, heterotrophy or osmotrophy. Obligatory autotrophs, requiring a light supply as a source of energy, suffer during the long winter.

Intrusion of pelagic *Ceratium arcticum* and *C. longipes*, recorded in the adjacent waters of Foxe Basin evidently did not occur in Igloolik. However, both species are considered as arctic and oceanic (Grøntved and Seidenfaden, 1935), and in the Newfoundland area they are described as essentially cold-water organisms (Frost, 1938). The absence of the large *Peridinium depressum*, found in both cold and warm waters of coastal and pelagic areas, might be explained to some extent in the same way as the absence of *Ceratium* in Igloolik. Probably it is mainly temperature and not salinity which primarily affects the geographical distribution of dinoflagellates, particularly *Ceratium* species (Graham, 1941). This is indicated also by the increase in population density and number of species of dinoflagellates from Igloolik southward towards Hudson Bay. Because dinoflagellates are transported by currents at different times and conditions, they are useful as indicators of the movement of water masses (Wood, 1954). Such

application cannot be practiced without new collection methods however, for dinoflagellates are rare in the arctic. The occurrence of new species, *Gyrodinium arcticum*, *Gymnodinium intercalaris*, *Cenchridium globosum* and *C. spherula* show that the taxonomy of arctic species should be more extensively studied before other problems can be solved.

TAXONOMIC DESCRIPTIONS OF DINOFLAGELLATES

Genus *Cenchridium* (Ehrenberg)

This genus comprises 4 species incorporated into the family Prorocentraceae (Schiller, 1933). Ehrenberg suggested affinities with Foraminifera. Bütschli considered *Cenchridium* as being associated with warm seas (from Schiller, 1933). The systematic position of the genus is not yet established because the organisms are rare and thus not readily available for study. Both species of *Cenchridium* found at Igloolik appear to be benthic forms occasionally brought into the plankton. The dorso-ventral organization of distinct ventral and dorsal valves occurs only in *C. globosum* (Fig. 15c, d). No intervalvar suture is found in *C. spherula* (Fig. 15b). Both flagellar pores are located at the front of the tube (Fig. 15a, c). The typical membrane pores, as in other Prorocentridae, are found in *C. globosum* (Fig. 15c), while in *C. spherula* parallel warts cover the membrane (Fig. 15c). This form is more elongated than those figured by Ehrenberg. Dimensions of *C. spherula* are $37 \times 27\mu$, of *C. globosum* $38 \times 20\mu$. Both species are not previously reported from the arctic. They have been found in the South Pacific (Schiller, 1933).

Gyrodinium arcticum n. sp. (Fig. 16a, b, c)

Body subspherical, asymmetrical and circular in cross section. Sulcus slightly sigmoidal, with a small cavity within the intercingular area, starting on the dorsal surface. Girdle ends prominently displaced. The left end of the girdle usually narrower, laterally oblique, dorsally straight. Sulcus deeply incised, with marked edges. Left lobe of hypocone ending with an acute, subcentrally descending notch and a noticeable margin within the epicone. Fine parallel and horizontal sutures forming distinct square or rectangular plates. Anterior flagellum emerging from the flagellar pore situated at the edge of the upper margin of the girdle. Sulcus deeply incised with marked edges ending as an acute notch where hypocone starts. Membrane surface covered with fine lines running both antapically and horizontally, the latter being less well defined, forming small plates of rectangular and square form. Regularly situated spherical inclusions within the membrane sutures. These inclusions absent within more densely distributed lines in the sulcus. Anterior flagellum starting at the upper edge of the girdle ridge as a flagellar pore. Posterior flagellum emerging at the level where the hypocone notch ends. A hyaline flap of the right hypocone lobe in some specimens covering the flagellar pore. Protoplasm dense, containing small

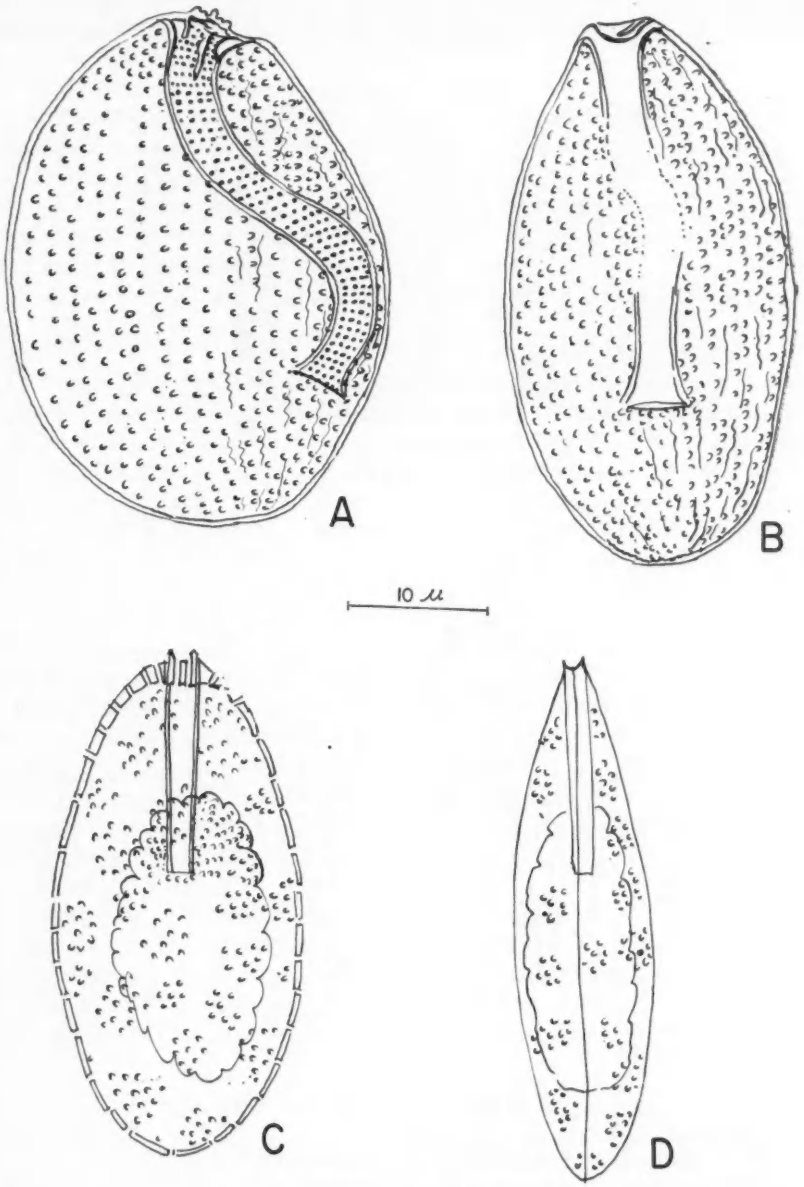

FIG. 15. *Cenchridium spherula.* (a) lateral view; (b) sagittal view. *Cenchridium globosum.* (c) lateral view; (d) sagittal view.

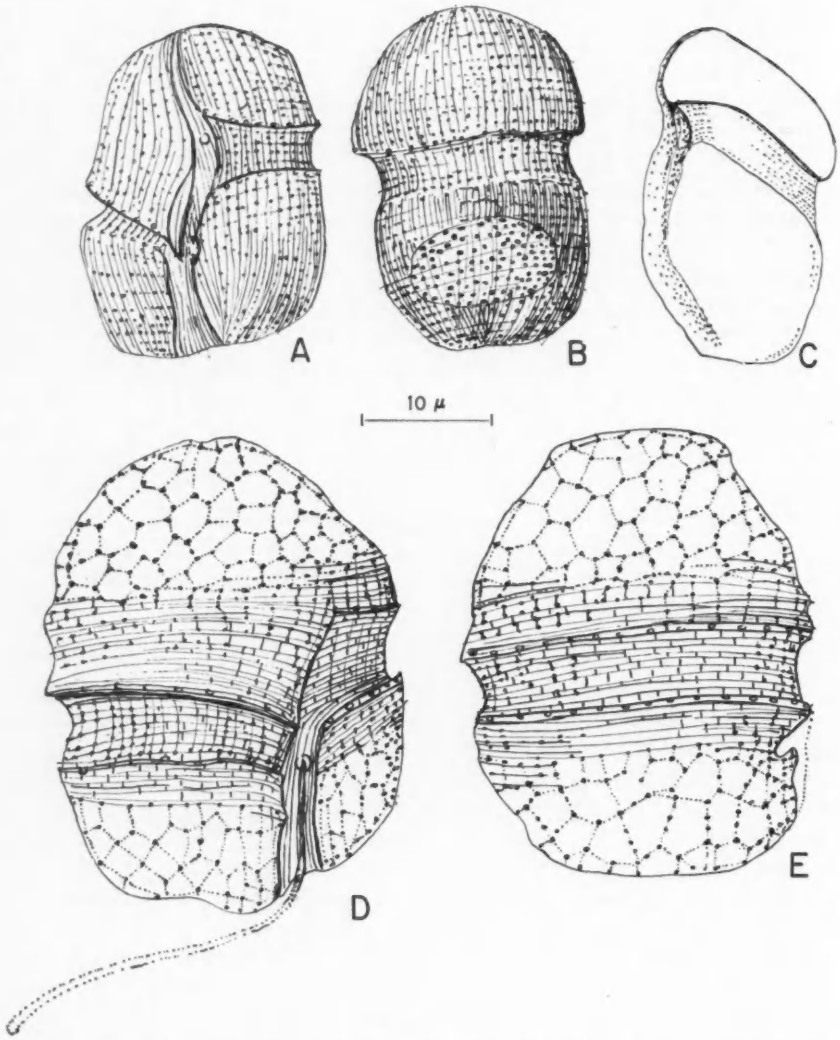

FIG. 16. *Gyrodinium arcticum* n. sp. (a) ventral view; (b) dorsal view; (c) ventro-lateral view. *Gymnodinium intercalaris* n. sp. (d) ventral view; (e) dorsal view.

globular inclusions. Nucleus subspherical with distinguishable chromosomes situated within the hypocone.

Dimensions: length 26–30 μ, breadth 20–28 μ.

Affinities: *Gyrodinium arcticum* appears to be distinct from a group of small and similar species such as *G. hamulus* Kofoid and Swezy, *G. grammaticum* Kofoid and Swezy, *G. incertum* Herdmann and many others insufficiently studied using only low microscope power. All aspects of the morphodynamics of this entire group have to be re-examined in order to establish a proper basis for taxonomic affinities of its members.

Occurrence: Igloolik, August 1956. Net and Utermöhl microscope samples.

Gymnodinium intercalaris N. SP. (Fig. 16d, e)

Body broadly rounded in most cells, subhexagonal in some. Subspherical in cross section with deeply impressed girdle and sulcus. Both ends of the girdle even or slightly displaced. Right section of the girdle three times broader than the left. Sulcus deep but short, ending within a deep edge of the girdle and not appearing within the epicone. Left lobe of epicone larger than the right. Left hypocone lobe twice as large as the right lobe. Epicone ending as an acute, strongly marked edge, clearly separated from the girdle, and protruding over the intercingular area. A small cavity beneath the left edge of the sulcus, visible in dorso-ventral position (Fig. 16e). Posterior flagellum emerging at the level of the left end of the girdle (Fig. 16d). Anterior flagellum not observed. Well marked equatorially located membrane sutures forming a wide belt of "circuli" in which vertical sutures also occur. These structures extending up and down from both sides of the girdle edges. Parallel lines in the sulcus, without horizontal sutures. Both surfaces of epicone and hypocone covered with large polygonal reticulum, containing spherical inclusions. Many suboval chromatophores observed in some cells while others appeared to be holozoic. Small inclusions found in protoplasm. Nucleus not observed.

Dimensions: 34–45μ.

Affinities: *G. intercalaris* may be easily identified by its "circuli", not observed in other forms. There is some similarity with *G. grammaticum*, but this form is distinct from it and other small *Gymnodinium* already described by Biecheler (1952), Hulburt (1957), and Schiller (1933, 1937).

Occurrence: Igloolik, September, 1956.

COCCOLITHINEAE AND OTHER FLAGELLATES

Great progress in our knowledge of Coccolithineae has been made since the introduction of the electron microscope. The taxonomic nomenclature of some groups has been changed (Braarud and Nordli, 1952; Halldal, 1953; Halldal and Markali, 1954; Braarud, 1955, 1955a; Braarud *et al.*, 1955). The light microscope permits only preliminary observations of the general features of Cocco-

lithineae. The final determination of coccoliths, including taxonomic identification, has to be completed with the electron microscope. In view of this the new taxonomic descriptions of Coccolithineae found in the Igloolik samples are given in a preliminary way only. It is thought that observations made here may be confirmed in the future by the electron microscope, as has happened with diagnoses by Schiller (1930), Lecal-Schlauder (1951), Chatton (1952), Deflandre (1952), and other others.

Coccolithineae are of less importance in the food chain economy of the arctic seas than in the warm seas where they are very abundant (Schiller 1930; Kofoid and Swezy, 1921). The maximum of Coccolithineae in Igloolik was represented by only 60,000 cells per litre, which is in great contrast to the populations of half a million cells per litre found in Hudson Bay (*Calanus* expeditions, 1953–54). There are probably more advantageous temperature conditions in Hudson Bay which particularly favour the development of larger populations of this flagellate.

Pontosphaera huxleyi LOHMANN (Fig. 9d)

Pontosphaera huxleyi was always a dominant component among other species of Coccolithineae. The low degree of calcification of coccoliths found in Igloolik seems to be associated with the low temperature, because such organisms from warmer waters appear to possess well calcified coccoliths.

P. huxleyi was a dominant species among the Coccolithineae. Its maximum appeared late in August, reaching 60,000 cells per litre. Owing to its small size it was identified with difficulty with the inverted microscope. It was more common than any other form of its group at Igloolik and in Hudson Bay. It seems to be common in northern seas (Braarud, 1935; Steemann-Nielsen, 1935).

Pontosphaera nigra SCHILLER (Fig. 9a-c)

Polymorphic form: Populations of this form consisted of spherical and subspherical specimens (Fig. 9a, b). Its spherical coccoliths were usually arranged irregularly, in some individuals densely and in others loosely. Each coccolith was built up of a spherical plate of 0.1 to 1.5μ diameter from which a fine stalk emerged. The length of the stalks varied from 1.5 to 3.5μ. The colour of the shell varied from dark brown to dark brown-yellow. The length varied between 3.5 and 24μ.

Occurrence: July to September, Igloolik.

Pontosphaera ditrematolitha N. SP. (Fig. 9e, g)

Spherical and subspherical cells easily distinguished by their large trematoliths, found mostly as 2 in each cell. Apart from large trematoliths, very small coccoliths also found. These arranged spirally (Fig. 9e) except in the apical area, where absent. The trematoliths of some cells with a large unperforated margin (Fig. 9e), while in some individuals, from 3 to 10 perforations observed. Such trematoliths in side view (Fig. 9g) deeply incised, and both their top and

bottom surfaces joined with a columella. Nucleus apical. Large lateral chromatophore. Single flagellum emerging from the apex.

Dimensions: spherical forms from 9 to 16μ, subspherical forms from 6 to 12μ.

Occurrence: August, Igloolik.

Syracosphaera sp. (Fig. 9h)

Some specimens of *Syracosphaera* sp. were observed with the inverted microscope and were also studied with the standard compound microscope. It was not possible to establish more detailed features, since it was not common enough in the collections. Single minute perforated coccoliths in some specimens covered almost the entire surface of the cell, or else were rare and dispersed. Two flagella of uneven size were seen in some specimens. A single chromatophore and a posterior nucleus occurred.

Dimensions: length from 6.5 to 11μ, breadth from 5 to 9μ.

Most of the cells were badly deformed and not suitable for identification purposes. It was rare in net plankton from August to September.

Pontosphaera sp. (Fig. 9i)

Mostly subspherical, seldom spherical, individuals of this organism were not observed in the motile stage. They were covered with tiny spherical coccoliths irregularly placed. Larger specimens of this form measured between 15 and 22μ. This organism seems to be closely related to *Coccolithophora pelagica*, described also from the English Channel by Lebour (1923). Single individuals occurred rarely in the net plankton in August.

Scyphosphaera sp. (Fig. 9k)

This was distinguished from *Pontosphaera nigra* by its pointed antapex and broad apex. Its coccoliths were of uneven length and heteromorphic, perforated and varying in size. Single coccoliths consisted of a discoid stalk and a stalk with distinct segments. Its calcareous shell was very fragile. Diameter from 10 to 15μ. Its taxonomical position is uncertain. It occurred in August.

Lohmannosphaera sp. (Fig. 9l, m)

These are subspherical cells, easy to distinguish by their apical appendages at the apex of which a usually dark dash-formed perforation is found. A thin fragile membrane of some cells contained two parietal chromatophores (Fig. 9l). In some individuals the cell membrane was colourless, in others, yellow-brown. The length of appendages was greater in larger forms, in which a large apical protuberance usually was formed (Fig. 9m), upon the surface of which dark perforations occurred. *Lohmannosphaera* sp., after treatment with 0.1% HCl, changed its colour to pale yellow and showed small bubbles associated with solution of the calcareous structure.

Dimensions: length of 9 measured specimens was between 15 and 28...

Occurrence: Igloolik, September.

Coccolithus pelagicus (WALLISCH) SCHILLER (Fig. 9n)

Shells were spherical or subspherical with wide apical openings. Coccoliths were large and elongated, sometimes with a distinct septum in the centre, and a narrow margin. In some specimens smaller coccoliths were found close to the apex, while the larger coccoliths were within the antapex. Some were constricted in the middle. Coccoliths were usually placed irregularly on top of each other. Igloolik specimens were similar to those found by Schiller (1930). Halldal (1953) reported it from the Norwegian Sea with a maximum of 16,500 cells per litre; Gaarder (1954) from the Atlantic. Holmes (1956) described it as not abundant from the Labrador Sea.

Dimensions: 32μ.

Occurrence: Rare in net plankton in August.

CHOANOFLAGELLATES

Salpingoeca natans Grøntved (Fig. 17a-h)

Two species of choanoflagellates, *Salpingoeca natans* and *Monosiga* sp., were occasionally found in the inverted microscope chambers and net hauls. Both organisms were most common on September 13, 1956, and occurred in small populations of 200 and 500 cells per litre. Thanks to Dr Jul. Grøntved, who kindly sent the author his original sample (No. 6583), taken at 20 m from the southern North Sea, it was possible to compare the Igloolik choanoflagellates with the original specimens. *S. natans* was reported from the Limfjord, Denmark, and from West Greenland. *S. natans* from Igloolik samples appears to be identical with those described from other localities by Dr Grøntved (1952, 1956). However some of the Igloolik individuals were larger. The main difficulty in identifying the Igloolik species was the absence of the outer collar in the majority of flagellates. Only a single collar, showing great morphological variability, was found (Fig. 17a-h). *S. natans* was finally determined when typical individuals with both collars were found (Fig. 17h). The organism is a highly variable one, as far as form and shape of collars is concerned. No stalk appeared in some individuals, which excrete mucus at their antapex, which serves for attachment upon a solid substrate (Fig. 17d). A fine square reticulum of lorica was observed without staining, but was accentuated with methylene blue, which also intensified tiny inclusions in intersections of the sutures. Some protomonades were attached by a small stalk to the inner side of the lorica (Fig. 17h). It was possible to distinguish a cell body from the lorica. A rectangular structure at the base of the outer collar seems to be associated with movements of the collar (Fig. 17h).

A single flagellum slightly longer than the entire length of the lorica with the stalk, emerged from the apex of the protomonade. A well distinguished nucleus was located centrally or subcentrally, containing a large nucleolus.

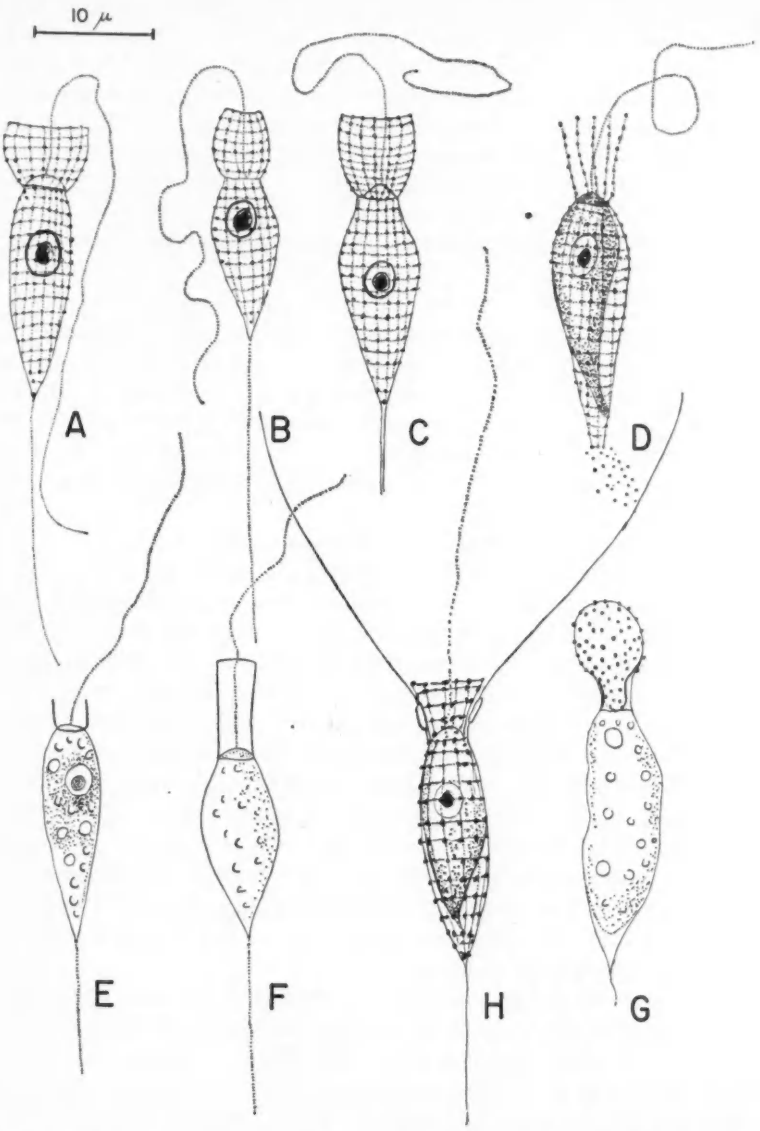

FIG. 17. *Salpingoeca natans.* (a, b) individuals with the long stalks showing fine reticulate structure of the lorica, flagellum and nucleus; (c) individual with short stalk; (d) individual without stalk, the protomonade attached to the wall of the lorica, with some mucus discharged at the antapex; (e, f) individuals with single collar; (h) individual with both outer and inner collar; (g) resting spore formation.

Spherical inclusions in the protoplasm represented reserve materials but were absent in some individuals. Finely diffused brown-green pigment was found in some cells and was most concentrated around the nucleus. It was also observed by the author in some choanoflagellates studied alive (unpublished data). Few individuals were found with the spherical structures attached to the apex, which appears to be a cyst formation. This requires more observations *in vivo*. *S. natans* was associated with a large number of bacteria which, as suggested, it may ingest as food, as observed in other forms.

Occurrence: In August and September more common than in other months.

Monosiga SP. (Fig. 18a-e)

A solitary elongated protomonade was attached to the antapical part of the lorica by a short stalk, and contained a nucleus with a nucleolus. The lorica consisted of three segments partitioned perpendicularly by 10 sutures. Its widely opened collar contained spherical inclusions, stained with methylene blue, within the intersection of the membrane sutures and within the edge of the outer collar. The flagellum was of varying length, usually shorter than the length of the body.

Dimensions: length 26μ, width 19μ (expanded collar).

Occurence: Rare, mostly found in August.

This species is similar to *Corbicula socialis* (Braarud, 1935), which is colonial, while this form is solitary. Its antapical sutures were well distinguished with front phase illumination. Three segments of the lorica were clearly cut out by the horizontal sutures. Ten antapical sutures divided the lorica into 30 distinct membrane areas, containing fine inclusions, wider within the apex and narrower within the antapex. *Monosiga* sp. appears however to be a distinct species since it shows different morphodynamic features which seem to be absent in the other known species. Final determination was not done because more information is required and its morphological variability should be investigated. It is possible that in some circumstances two collars could be formed in this *Monosiga* as was found in *S. natans*. The possibility of two collars has to be taken into account, since *Diplosiga* sp. (Grøntved, 1956) has two collars and this form seems to be quite similar to the Igloolik organism.

Some details of cell division were observed, showing that both daughter loricas are joined by the edges of their umbrellas, while both protomonades are still joined by a single flagellum (Fig. 18d). The triangular and barrel-like shapes of the loricas in dividing specimens indicated that these are not rigid structures but are able to perform some movement. Some of the protomonades were found separated from the antapical part of the lorica and were freely floating in the plankton (Fig. 18b). *Monosiga* sp. appears to be a non-obligatory plankton organism which can also float freely in plankton or be attached to the surface of diatoms (Fig. 18a).

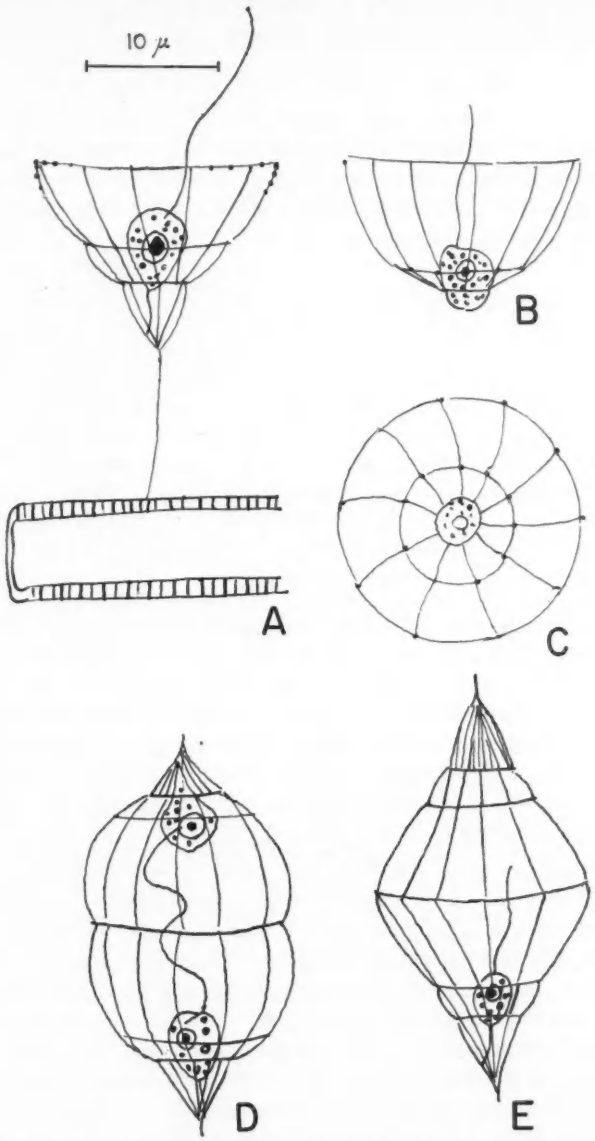

FIG. 18. *Monosiga* sp. (a) an epiphytic individual upon diatom surface; (b) motile individual consisting of the protomonade and upper parts of lorica; (c) observed in front view; (d) two daughter-individuals with a single unseparated flagellum; (e) two daughter-loricas after completed division, of different shape than (d); containing only a single protomonade.

OTHER FLAGELLATES

Some other flagellates found in the Igloolik samples were not abundant enough to be studied in all details. They were identified as *Bodo* sp. and as *Lepocinclis* sp., epiphytic on *Achnantes*. Since *Lepocinclis* Lemmermann (1908) belongs to a freshwater group, it must here be specially adapted physiologically to the marine environment. It was observed in March, when only very poor plankton was observed (Fig. 19).

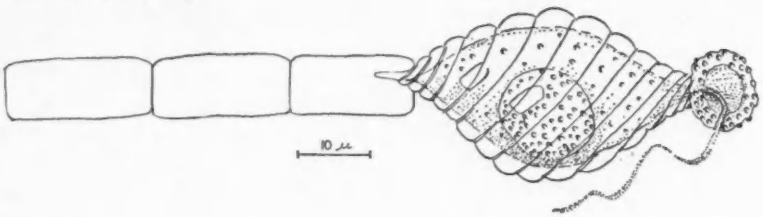

FIG. 19. *Lepocinclis* sp. An epiphytic individual on the membrane of the diatom *Achnantes taeniata*.

CILIATES

Among eleven species of ciliates (identified from Leegaard, 1915) found at Igloolik, *Mesodinium rubrum*, *Lohmanniella oviformis*, and *Laboea conica* were more common than Tintinnidae. Populations of ciliates seldom exceeded a few hundred individuals per litre. The scarcity of species and their small populations seems to be caused by the long period of low temperatures and hydrographic uniformity of the Igloolik shelf. In Hudson Bay (unpublished data) where 27 species were found and greater populations of ciliates occurred, biological conditions appear to be more advantageous. The number of ciliates (28) found in Denmark Strait (Braarud, 1935) is very close to that found in Hudson Bay, while the number (34 species) in Greenland waters collected by Seidenfaden is somewhat higher. It is however not the number of species but the higher total crop per litre which is typical of the higher productivity standard of other geographical areas quoted here. The mean number of ciliates collected at the four depths was 671 individuals per litre. The mean for the surface samples was 135 per litre; there were 148 at 10 m, 268 at 25 m (the maximum), and 120 at 50 m. The seasonal occurrence of ciliates (Fig. 8) shows a late maximum in October and a lower peak in August. When crops of ciliates at Igloolik are compared with populations of single samples from the Norwegian Sea, where 14,200 were found per litre (Halldal, 1953) or with a Labrador Sea sample of 17,200 *Laboea conica* per litre (Holmes, 1956), the low productive level at Igloolik is obvious. Ciliates appear to be effective grazers. Little is known of their individual grazing capacity. They ingest flagellates, diatoms and copepod eggs.

GRAZING

Grazing by herbivorous zooplankton upon phytoplankton is recognized as a significant factor in reducing the size of populations (Steemann-Nielsen, 1935; Braarud, 1935; Fleming, 1939; Riley, 1946, 1953; Riley and Bumpus, 1946; Cushing, 1955). Comparisons of the phytoplankton and zooplankton cycles at Igloolik and Scoresby Sound, Greenland, show that similar general features occur in both areas. It is difficult to make closer estimates since different methods were used in both areas. Data from Igloolik show that the spring increase in phytoplankton and zooplankton occurred almost simultaneously. The increase in phytoplankton and in the number of copepod nauplii (the major herbivores) in April is evident. The commonly described gap between phytoplankton and zooplankton summer maxima does not appear in the Igloolik cycle where the interval, if real at all, does not exceed more than a few days.

The rapid decline of diatoms at Igloolik in the autumn is related to the end of the summer season and increased grazing of great populations of zooplankton. The simplified scheme of grazing in seas usually shows phytoplankton as the main biomass producers and all herbivorous animals as feeders. It is true, but we find that the ciliates and the holozoic flagellates must be also of importance as grazers, and they are not included as a grazing link. The holozoic Gymnodinioideae, which are able to ingest diatoms, Coccolithineae or ciliates (Fig. 7, 14), are significant grazers since they can appear in larger populations per litre than zooplankters. The complexity of grazing has many aspects (Cushing, 1955) which preferably should be studied in the field. In the arctic it is of particular interest to estimate the under-ice film of diatoms found in spring and summer, and probably in winter.

Preliminary investigations were made by the author in order to estimate the intensity of grazing during various seasons as shown by the number of fecal pellets produced by different plankton animals from preserved and unpreserved samples. For such purpose a larger volume of sea water than was used here has to be examined. As the largest number of pellets occurred in August and September, this is the season of most intensive grazing in the arctic. Some of the pellets contained single *Chaetoceros socialis* frustules, while others consisted of empty thecas of *Peridinium* and *Goniaulax*. Both were apparently selectively grazed. The unknown animal whose pellets contained dinoflagellates which were absent in net and quantitative samples, shows great efficiency as a grazer in finding such rare food. The fecal pellets of the omnivorous grazers contained frustules of many diatom species. The number of feeders and size of standing crop of phytoplankton fluctuates according to the seasons, hydrographic conditions, and biodynamics of herbivores. Estimates from Scoresby Sound (Digby, 1953), compared with Igloolik data (Grainger, 1959), show that the size of populations of zooplankton in both areas was similar. The quantitative estimates of the phytoplankton crop show that a hungry season for herbivorous animals began in mid-September and ended in mid-May. This was a period of 8 months, during which fats previously deposited in animal tissues were utilized. It seems possible, however, that many animals may feed on microflora and microfauna of the benthos or turn to cannibalism.

MAIN FEATURES OF THE IGLOOLIK PHYTOPLANKTON

The character of the phytoplankton and its hydrographical background in the Igloolik area cannot be dealt with in isolation, since similar features probably exist within a wide region of coastal Foxe Basin as well as in higher arctic latitudes. The main limiting factor for the marine life at Igloolik is the long duration of fast-ice, which by freezing and melting affects salinity, light penetration and temperature. Shallowness and fast-ice conditions appear to increase the arctic oligotrophy within the wide area where the hydrographical uniformity is caused by a limited water mass exchange with other localities. The phytoplankton populations of the Igloolik station appear to be largely autochthonous because the area concerned is away from the main course of the Fury and Hecla current and mixing is limited. The inflow of this current is directed by the Bouverie Islands towards the southwest side of northernmost Foxe Basin, while its smaller ramification goes through Richards Bay which is very shallow and is covered in some places by grounded ice. This factor minimizes intrusion of Fury and Hecla waters and foreign phytoplankton populations. Allochthonous phytoplankton populations may probably enter within the wide area between Igloolik Island and the Melville Peninsula coast during tidal changes and southeasterly wind activity. The pelagic element is particularly rare, and represented by *Chaetoceros atlanticus*, *Ch. decipiens*, *Ch. lorenzianus* and *Ch. subsecundus*. It seems not to be native to Igloolik, having presumably drifted into the area from the south. The scarcity of warm-water forms like Coccolithineae and dinoflagellates, and the preponderance of arctic and cosmopolitan diatoms, represented by 74 species, indicates ecological features which can be found elsewhere in northern waters. Benthic diatoms were rare, represented by 8 cosmopolitan species, which were noticed more frequently and in larger populations in the Hudson Bay phytoplankton than at Igloolik. The mud-covered bottom of Igloolik does not favour the development of microflora and algae, since only a single rhodophycean, *Phyllophora brodiei*, was taken with the Van Veen bottom sampler. Adjacent Turton Bay appears to be richer and more favourable for both zoobenthos and phytobenthos.

DURATION AND SUCCESSION OF PLANKTON SPECIES

The length of time during which some plankton organisms remain in the floating planktonic phase depends upon the completion of their life cycle. Because the optimum conditions for growth in the arctic are restricted to a few months, the majority of planktonic forms have to complete their cycles in a short period of time. The arctic diatoms soon disappear from the plankton after cyst formation (Gran, 1904). This was observed also at Igloolik, but it was applicable mainly to the brackish neritic diatoms, including melting-ice species.

The pelagic forms like *Chaetoceros atlanticus*, *Ch. borealis* and *Ch. teres* persisted for a much longer period of time in the plankton than those which formed resting spores. The frequency of occurrence of pelagic forms was lower in the sedimentation chambers than in the net samples, in which they appeared continuously even in winter when vertical dispersal affected the number of species in net and sedimentation chambers.

Plankton elements are placed in groups according to the length of time which they spend in suspension in the water (Fig. 6, 20). Those which remained in plankton the entire vegetative season include: *Achnantes taeniata*, *Fragillaria cylindrus*, *Nitzschia seriata* and *Thalassiosira nordenskjøldi*. The others showed a gradually shorter duration in plankton, and include: *Nitzschia closterium*, *Denotula confervacea*, *Nitzschia* sp., *N. grani*, *Chaetoceros decipiens*, *Nitzschia pungens*, *Melosira islandica*, *Lauderia glacialis*, *Eucampia zodiacus*, *Thalassiosira rotula*, *Th. gravida*, *Chaetoceros compressus*, *Ch. affinis*, *Ch. constrictus* and *Navicula pelagica*. The group of shortest duration is represented by *Chaetoceros septentrionalis*, *Ch. debilis* and *Bacteriosira fragilis* (Fig. 21). Diatoms,

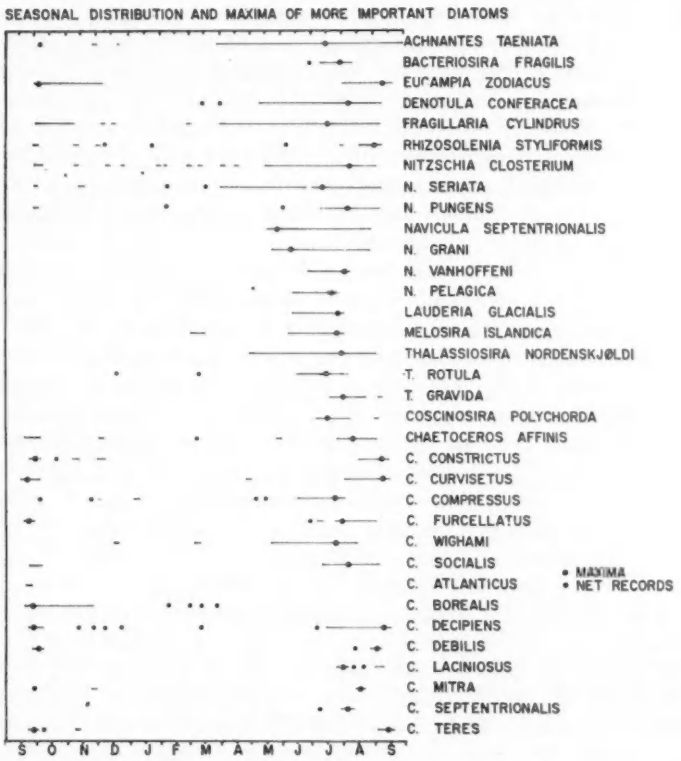

FIG. 20. Seasonal distribution and maxima of the more important diatoms.

as compared with dinoflagellates, flagellates and ciliates, show a distinct dominance.

Seasonal succession in plankton has probably many causes; noticeable in spring are diatoms, and in summer, dinoflagellates. Early spring diatoms were determined as arctic and the latter as boreal. The trend of succession depends upon composition of the initial stock at any time, and it may vary from year to year (Braarud *et al.*, 1953). Apart from the environmental factors, some phytoplankton species can inhibit or stimulate growth of other species by diffusion of metabolites into the water (Rice, 1954). It is thought that diffusion of metabolites may affect not only the size but also the succession of some species. How such biochemical warfare is carried out among different species in the seas is completely obscure. Conover (1956) studied successions of Long Island Sound.

Margalef's (1957) data from Rio Vigo (Mediterranean) show 3 or 4 complete successions of regular pattern, hardly distorted by local irregularities. Winds and tides have hardly any effect upon a pattern of succession. The author is convinced that an arctic type of succession is repeated from year to year, but it could be distorted by turbulence or other factors, as particularly observed at Point Barrow, Alaska (author's unpublished data). The idea of biogeographical regionization and the use of succession for the ecological analysis of plankton and productivity of the arctic (Bogorov, 1958) appears to be useful in its application.

Observations made in different arctic latitudes (Braarud, 1935; Steemann-Nielsen, 1935; Shirshov, 1938; Bogorov, 1938, 1958, 1958a), when contrasted with the Igloolik data, indicate many differences concerning quantitative features of primary production, taxonomic composition and species successions. Davidson's (1931) observations in Hudson Bay on early development of phytoplankton are not sufficient to show annual successions.

Phytoplankton succession in Denmark Strait, begun with flagellates, was continued by *Achnantes-Fragillaria* and *Thalassiosira-Chaetoceros* vegetation, poor populations of *Denotula*, and dinoflagellates (Braarud, 1935). The pennate diatoms appeared in early summer while *Chaetoceros* with dinoflagellates occurred later in the season in the East Greenland current (Steemann-Nielsen, 1935). A succession of *Thalassiosira gravida*, *Fragillaria oceanica*, *Achnantes taeniata* and *Denotula confervacea*, observed by Shirshov (1937; after Bogorov, 1958a) in the arctic seas, was classed as a group of spring species, which were followed by the late-spring species *Chaetoceros furcellatus* and the summer species *Ch. debilis*, *Ch. compressus*, *Ch. diadema*, *Ch. mitra* and *Ch. teres*. Dinoflagellates increased in number as the season advanced. An early spring succession in East Greenland (Digby, 1953) began with *Nitzschia frigida*, *Amphiprora hyperborea*, *Navicula septentrionalis*, *N. grani*, *N. pelagica*, *Fragillaria oceanica*, *Thalassiosira nordenskjöldi* and *Th. gravida*. Because different methods were applied by investigators, the above considerable differences in results have to be expected. Except for flagellates, similarities in the successions were observed between Denmark Strait and Igloolik. All other references indicate in general similar sequences of spring Pennatae, summer Centriceae and dinoflagellates. In the main outlines, succession of the taxonomic groups appears to be repeated within a similar general

pattern established by ecological niches and dynamics of individual species of phytoplankton.

In September 1955 and 1956, Centriceae were represented by 13 species, which obviously dominated the Pennatae. A similar situation occurred in October. The unbalance between Centriceae and Pennatae began in November and continued throughout the winter until the end of April. Initial spring populations under the ice were observed in the late days of April and they started with *Achnantes-Fragillaria* increasing in numbers, associated with initial populations of *Denotula*, *Navicula*, *Nitzschia* and a small number of *Thalassiosira*. Though *Achnantes-Fragillaria* still dominated in early June, the secondary *Denotula-Navicula* grouping became more significant. The decline of "shade" Pennatae took place after July 15, and marked the climax of *Achnantes*. The Centriceae rapidly increased in number of species and size of population. *Chaetoceros* species became most significant until the climax of the Centriceae was reached on August 20. The ribbon-shaped Pennatae constituted a main spring succession, extending into early summer, and became gradually replaced by the summer phase of diatoms, represented by the dominant Centriceae, and late summer dinoflagellates. The comparisons point to the phytoplankton of the waters west of Greenland showing close similarities to Igloolik phytoplankton in the seasonal succession of species (Grøntved and Seidenfaden, 1938). When the ice breaks at Igloolik, a rich plankton, chiefly of *Fragillaria*, is developed. It is replaced later by *Thalassiosira*, and later still by a number of *Chaetoceros* species and the Peridineae. The central Labrador Sea, which is characterized by oceanic species, has a succession distinct from that of Disko Bay, Greenland.

The annual phytoplankton cycle at Igloolik is of the "bimodal" type (Fig. 3). The spring "shade" pennate diatoms exhibited their climax sooner than the summer Centriceae. There was a gap of 28 days which separated the climaxes of Pennatae and Centriceae (Fig. 3). It is sufficient however to classify the annual cycle at Igloolik as the "bimodal" type, in contrast to the "unimodal" type described as typical for the high arctic by Bogorov (1958). Since the net crop, which is recognized as insufficient by the majority of authors, was mainly used for establishing the high arctic type of phytoplankton cycle, the determination of successions of the arctic phytoplankton still remains an open problem in different latitudes. The final solution could be achieved by the use of sedimentation methods and nets allowing quantitative analysis of common and rare species.

BIOLOGICAL SEASONS IN PHYTOPLANKTON OF ARCTIC SEAS

The determination of the biological seasons in the sea has to be based upon principles other than those applied to the higher plants rooted in soil. The seasonal variation in qualitative composition and abundance of organisms permits us to distinguish biological seasons (Bogorov, 1938). Arctic biological winter is characterized by a minimum number of organisms, especially phytoplankton species. Biological spring starts with a slow increase of phytoplankton beneath

the ice. The short biological summer is characterized by an abrupt decrease of autotrophic populations at the end of the season.

Halldal (1953) distinguishes in the Norwegian Sea: winter, from December to March; spring, lasting until June; summer, lasting until September; autumn, from September until October or the beginning of November.

The scheme of biological seasons in the far north made by Bogorov (1958) has been supplemented by the introduction of data from Scoresby Sound, East Greenland (from Digby, 1953) and recent observations from Igloolik (Fig. 21).

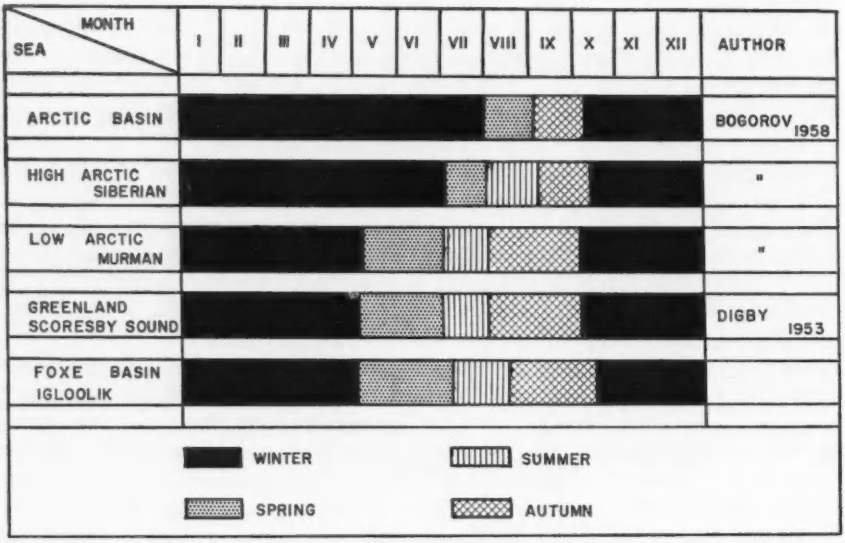

FIG. 21. Duration of the arctic phytoplankton seasons.

The high arctic seas (polar basin and Siberian polar seas) are characterized by a single maximum of phytoplankton. This biological spring corresponds to the calendar months of July and August. In the polar basin the maximum of phytoplankton occurs in August, and in the Siberian Seas in the latter half of July (Shirshov, 1938; after Bogorov, 1958a). The western Barents Sea has two maxima; the biological spring corresponds to the month of May, the biological autumn to August. The more severe winter extends up to 10 months in the arctic basin. Biological spring in the Murman area starts approximately at the same time as in Scoresby Sound or at Igloolik. The duration of biological seasons in the arctic seas (Fig. 21) shows little difference among the regions considered. The beginning of phytoplankton revival after winter has to be related to local ice conditions which vary greatly from year to year from area to area.

Sverdrup (1954; from Marshall, 1958) suggests that phytoplankton production starts in April on the Bear Island Bank and in June in the deeper Atlantic water, and second that as the ice recedes to the northeast over the Central Bank, an outburst of phytoplankton takes place in its wake. In the shallow waters of Igloolik and in Scoresby Sound, Greenland, the spring increase of phytoplankton starts at approximately the same time. It was Ross (1954) who observed that arctic diatoms start to grow even earlier, in March. The under-ice film of pennate diatoms taken in March 1957 in the Gulf of St. Lawrence, by the Atlantic Oceanographic Group, consisted of 32 species that are considered as arctic shade plankters (unpublished data). It is obvious that the plankters had started to grow earlier in the winter darkness. The spring outburst takes place at different times in open and in protected coastal areas (Grøntved and Steemann-Nielsen, 1957). Although the biodynamics of arctic phytoplankton possess their own features, these appear not to be a function of geographical latitudes in the main, as Graham (1941) suggested, but a question of nutrient addition with newly introduced water. We can agree that the intrusion of waters rich in nutrients may invigorate growth of phytoplankton if it takes place during the light optimum required for photosynthesis.

SOME REMARKS ON THE CHARACTER OF THE ARCTIC PHYTOPLANKTON

The pioneer works of Gran (1904, 1908, 1912), Cleve (1873, 1896) and others have been concerned mainly with taxonomic problems of phytoplankton, and its distribution in the arctic. The new approach to the biogeographical divisions of phytoplankton has been applied by Braarud *et al.* (1953). The available data of Polunin (1934), Grøntved and Seidenfaden (1938) and Ross (1954) bring many facts to light on the geographical distribution of phytoplankton species.

The arctic biotope is best characterized by the presence of ice and its ice microflora. It is obvious that the arctic ice flora can flourish in subarctic waters, where they can persist for a rather long period of time. No distinction between the arctic and subarctic can be made, as yet, on the basis of phytoplankton distribution.

Data available (unpublished data) indicate that the biogeographical distribution of phytoplankton is not a function of temperature only, but of both temperature and light. It is obvious that a group of diatoms forming a large population under the ice may be considered as a "shade" flora, if it is absent where there is no ice, and therefore typical for the arctic environment. Steemann-Nielsen, from his results of Carbon-14 investigations, concluded that light adaptation of phytoplankton is possible, and Steemann-Nielsen and Hansen (1959) concluded that "none of the many plankton surveys from the arctic has shown any indication of the occurrence of a special 'shade' flora". Large

populations of the flagellated organisms found by Rodhe (1955) beneath the ice of a subarctic lake in Sweden in winter must be considered as a "shade" group. Obviously the ribbon-shaped Pennate diatoms found in April beneath the Igloolik ice were grown under ice impenetrable by light, and must too be classed as a "shade" flora.

It is however possible that there is a considerable light adaptability in arctic diatoms which can flourish in almost any light condition found in the arctic, if nutrients are available. The Centriceae diatoms, most abundant during the open water period, where maximum light is available, may be contrasted with the "shade" Pennatae as a "sun" flora. Possibly the succession of the spring "shade" by the summer "sun" group of diatoms has been induced by different physiological requirements in each group. Diatoms are dominant in the dark arctic environment, because they can tolerate long periods of darkness at low temperature.

The size of the phytoplankton populations and their taxonomic composition is a good ecological indicator for classification of waters in different latitudes. The total list of phytoplankters from Igloolik includes 121, in the slightly warmer Hudson Bay it is 235 (unpublished data). In the region of Point Barrow, Alaska, the number of species was still higher, 286 (unpublished data). The number of dinoflagellates reflects particularly well what is said above. They increased from 32 species found in Igloolik to 91 found in Hudson Bay (unpublished data). The increase of flagellated groups from north to south is related to the weakening grip of severe arctic conditions, to the increase in temperature and in solar radiation found towards the south. Not nutrients but temperature mainly favours developments of dinoflagellates (Gran, 1912; Graham, 1941; Wood, 1954). Preponderance of flagellates over diatoms in the southern latitudes is exemplified well by the plankton list of Rampi (1945) from San Remo, Monaco, where 350 species occurred, 245 of them dinoflagellates. I believe therefore, that the character of the ecological conditions of ocean waters could also be determined from the biological balance shown by the quantitative relationship of diatoms and flagellated organisms.

SUMMARY

1. A collection station was situated at 69° 20.5′ N, 81° 43.5′ W on the coastal shelf of the northern part of Foxe Basin. This area was covered for about 9 months by fast ice, a limiting factor for phytoplankton life.
2. Sea water samples for phytoplankton, studied by the sedimentation method, were collected about twice a month from September 1955 to September 1956, at the surface, 10, 25 and 50 metres depth. Vertical net hauls for taxonomic examination were also taken. Interpretation of temperature, salinity, oxygen and phosphates was also made.
3. The predominance of low temperatures (within a range of 3°C), and ice and light conditions influence the taxonomic composition of the phytoplankton

and the size of its populations. The absence of various taxonomic elements and some uniformity of general phytoplankton features seems to be related also to a small degree of communication by currents with other adjacent areas.

4. The vertical occurrence of phytoplankton at Igloolik was greatly differentiated in the course of the season. Phytoplankton populations at the surface from April 26 to May 19 were nearly equal to those found at 10 m. They became slightly higher in June, and were markedly lower in July, then increased when the effect of melting ice and low salinities had diminished.

5. Although maximum phytoplankton production was at 10 m, the trophogenic layer in the ice-melting period presumably started from about 2 metres depth and extended down to about 15 m. Below 10 m phytoplankton populations diminished with increasing depth.

6. Four biological season were distinguished at Igloolik. *Spring* started in April, with an *Achnantes-Fragillaria* bloom, and lasted until July. It was marked by maxima of the pennate diatoms, succeeded in early summer by the Centriceae. The climax of the Pennatae appeared on July 15, that of the Centriceae on August 11. The latter coincided with maxima of dinoflagellates and Coccolithineae. *Summer* began at approximately the end of July, with increasing populations of Centriceae. September and October represented *autumn*, marked by cessation of metabolic activities. The biological *winter* lasted from November until April.

7. Since the majority of the numerous brackish-neritic diatoms were metabolically passive because of cyst formation, they were often associated with low oxygen content of the water.

8. A taxonomic list of species is given. Three new species, *Gymnodinium intercalaris*, *Gyrodinium arcticum*, and *Pontosphaera ditrematolitha* are described. For the first time two rare and little known species, *Cenchridium spherula* and *C. globosum*, were noticed in the plankton of arctic waters. Nine Coccolithineae, two Choanoflagellates and a few little known flagellates were also studied in detail.

9. The quantitative dynamics of phytoplankton populations and their vertical occurrence were contrasted with those of other geographical latitudes.

10. The general taxonomic composition of the Igloolik phytoplankton seems to be greatly influenced by the severe ice conditions associated with poor light supply, hydrographical uniformity and shallowness of the area.

11. The holozoic dinoflagellates were dominant in the Igloolik samples, while brown autotrophic species formed only small populations. The strong-membrane Peridineae and Dinophysideae were represented also by colourless holozoic forms which produced still smaller populations, presumably resulting from light and temperature slowing down their metabolic processes.

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A Preliminary Study of the Energy Budget of Lake Ontario[1]

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ABSTRACT

Recent bathythermographic surveys carried out on the research vessel *Porte Dauphine* have provided estimates of heat content for Lake Ontario and permitted a preliminary study of its energy budget. The imbalance between the absorbed short wavelength sun and sky radiation, and the losses due to evaporation, sensible heat conduction and net long wavelength back radiation, result in heating of lake water from March to August and cooling from September or October to February. The peak heat content lags the peak surface temperature by about one month. The amount of energy advected into the lake is relatively small compared with other terms in the energy budget. Thus, energy budget calculations do not depend upon the accuracy with which the water budget is known. The principal difficulty in applying present techniques for determination of an energy budget is lack of meterological data over the lake surface.

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INTRODUCTION

THE DETERMINATION of the energy exchange between bodies of water and air constitutes one of the principal problems of oceanographic and limnological studies. Oceanographic studies of the energy budget are utilized for problems in seasonal temperature distribution, transport of energy by currents and the determination of water evaporation for quantitative calculations of elements in the hydrologic cycle (Sverdrup *et al.*, 1942). Limnological work has been undertaken principally for water loss investigations in reservoirs (see, for example, U.S. Geological Survey, 1954) and for predicting lake levels.

The present study was undertaken to determine the applicability of the energy budget method to the Great Lakes for the calculation of evaporation and the study of seasonal temperature changes.

In 1953 Blust, in an unpublished report of the United States Lake Survey, considered the various methods for determining evaporation, concluded that " . . . the heat budget method is superior for application to the Great Lakes . . . ", and made specific recommendations for carrying out initial studies. However, it has not been possible previously to make even a preliminary estimate of the energy (heat) budget for any of the lakes because of paucity of data and lack of continuity in observation. When, in 1958, R/V *Porte Dauphine* was made available on loan to the Ontario Department of Lands and Forests by the Royal Canadian Navy it became possible to start to supply the data and the continuity, to begin with, on Lake Ontario, for energy budget studies among other things. Presentation of some of the results was made by Bruce and Rodgers (MS, 1959).

The factors that must be considered in the energy budget are: short wavelength incident sun and sky radiation; reflected sun and sky radiation; long wavelength net back radiation; energy storage in the lake; energy contributions from inflow and outflow (including rain, rivers, snow and seepage); conduction of sensible heat and the energy used in evaporation. In this report all but the conduction and evaporation terms are evaluated individually with available data and by application of semi-empirical formulae presented in the literature. The sum of the conduction and evaporation terms is determined by balancing the energy budget (see equation 2) and dividing this sum between the conduction and evaporation processes in accordance with Bowen's ratio (Bowen, 1926; Sverdrup *et al.*, 1942).

Estimates of the average heat storage in the lake have been provided by bathythermographic surveys carried out on the *Porte Dauphine* during 1958 and 1959. These provide energy storage figures for late spring, summer and early fall periods in Lake Ontario. For winter months, the surface temperature data presented by Millar (1952) have been utilized, in conjunction with two assumptions concerning the vertical and horizontal temperature distribution within the lake, to provide energy storage figures.

Over-winter cruises were made for the first time in 1959–60, and heat content data from these have been included. As only one complete winter's data are available, and since that winter's air temperatures were somewhat milder than

normal, not as much weight was given these 1959–60 figures in comparison with the long-term meteorological averages and Millar's figures.

The energy budget calculations provide an estimate of the evaporation of water from the surface of the lake. The energy budget method is the third method to have been used to determine evaporation from Lake Ontario. The two methods used previously were the water budget and mass transfer methods (Hunt, 1959; Morton and Rosenberg, 1959; Kohler, 1959; Snyder, MS, 1960) and so the results from eight evaporation studies can be compared, providing a further check on energy budget results.

THE ENERGY BUDGET

General Equations

The energy budget for a specified time interval is expressed in the following equation:

$$Q_s - Q_r - Q_b - Q_h - Q_e + Q_v - Q_t = 0 \quad \ldots \quad (1)$$

Q_s is the amount of solar radiation incident to the water surface, Q_r the reflected solar radiation, Q_b the net back radiation, Q_h the conduction of sensible heat to the atmosphere, Q_e the energy in evaporation (or condensation), Q_v the net advected energy, and Q_t is the energy storage of the body of water considered. Energy abstracted and produced by chemical or biological activity, and heat exchange with bottom sediments are considered negligible.

In equation (1) values of Q_s, Q_r, Q_b, Q_v, Q_t can be obtained from meteorological and limnological measurements, so giving $(Q_h + Q_e)$. Similarly, from a relationship due to Bowen (1926), the ratio:

$$Q_h/Q_e = R \quad \ldots \quad (2)$$

can be determined independently, and then Q_h and Q_e each can be determined.

The accuracy of application of (2), in the present circumstances, is considerably less than the accuracy of the terms in (1) so that obtaining independent knowledge of either Q_e or Q_h would be a great advance.

Monthly means of daily values have been employed to give an average yearly cycle, and the terms in equation (1) were calculated in energy flux units of gram calories per square centimeter per day (g-cal/cm^2/day).

The bathythermographic surveys were carried out in 1958, 1959 and 1960 whereas the surface temperature data given by Millar, and used here in the calculation of Q_t, Q_e and R, represent the period 1937–1946. Since these data do not necessarily represent similar periods, they have been uncritically coupled with long-term averages of meteorological elements at land stations around the lake. Meterological data are required in the calculation of every term but Q_t.

The bathythermographic surveys covered all but the shallow outlet basin region in the east end of the lake (the region north of the Main Duck Islands), and so only the larger and deeper portion of the lake has been considered. The consequence of the outlet basin in the budget of the whole lake will await further study. Since shallow basins such as Saginaw Bay in Lake Huron and Green Bay in Lake Michigan, and the Lake Ontario outlet basin, may contribute heat

out of all proportion to their areas (and volumes), the neglect of the outlet basin in this case may be somewhat serious. A chart of the lake and the station pattern for 1959–60 surveys are shown in Fig. 1.

Incident Solar Radiation—Q_s

Monthly values of cloudless-day solar radiation and average daily incident solar radiation were obtained from charts prepared by Mateer (1955 a, b). A comparison of the two values for each month shows the effect of cloud cover on the incident solar radiation (see Fig. 2).

Some indication of the variation in incident radiation, from year to year, is shown in the figure by standard deviations derived from 20 years of radiation data (1938–1957) at Toronto, Ontario. The variation from year to year is caused principally by differences in cloud cover.

Reflected Solar Radiation—Q_r

The reflectivity or albedo of a water surface under various sun altitudes, cloud heights and cloud amounts has been determined by Anderson (1954) in the Lake Hefner study. The average altitude of the sun for each month has been obtained by interpolation from tables in the Climatological Atlas of Canada (Thomas, 1953). Reflectivity was obtained from Anderson's graph for broken cloud conditions. Since Lake Ontario develops little ice cover, the amount of reflected radiation is a small portion of the energy budget.

Net Back Radiation—Q_b

Net back radiation is the resultant longwave radiation exchange between the water and the atmosphere. It is dependent upon air and water temperatures, the water vapour content of the air, cloud heights and cloud cover. The Lake Hefner study (Anderson, 1954) resulted in a semi-empirical equation for atmospheric radiation which, when combined with the value for emissivity of water determined for that study (i.e., 0.970 ± 0.005) and corrected for reflected atmospheric radiation, may be summarized into the form (Tabata, 1958):

$$Q_b = 1.141\ [T_w^4 - T_2^4(a + be_2)] \times 10^{-7}\ \text{g-cal/cm}^2\text{/day} \qquad \ldots (3)$$

where T_w and T_2 are the absolute temperatures of the lake surface and air, respectively, at 2 metres' height, and e_2 is the vapour pressure of the air in millibars at 2.0 m. The parameters a and b take on values dependent upon cloud cover and cloud height found from empirical expressions given by Anderson (1954),

$$a = 0.740 + 0.025\ Ce^{-0.584h} \qquad \ldots . (4a)$$

$$b = 0.00490 - 0.00054\ Ce^{-0.060h} \qquad \ldots . (4b)$$

where C is the cloud amount in tenths, and h the cloud height in thousands of feet.

Ten years of cloud height data (1949–58 inclusive) for Malton airport, which is 12 miles northwest of Toronto and 8 miles inland, were analyzed by the Data Processing Section of the Canadian Meteorological Branch for 0, 1 to 5, 6 to 9

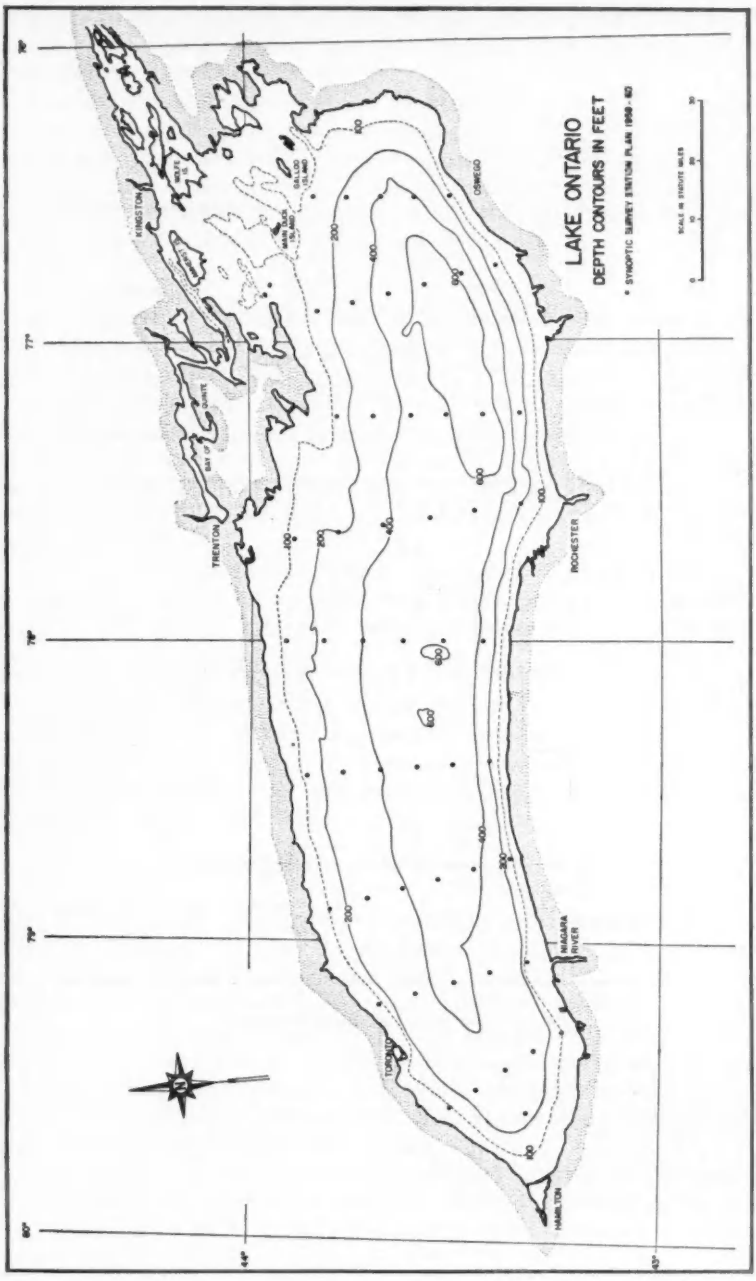

FIG. 1. Depth contours and station locations.

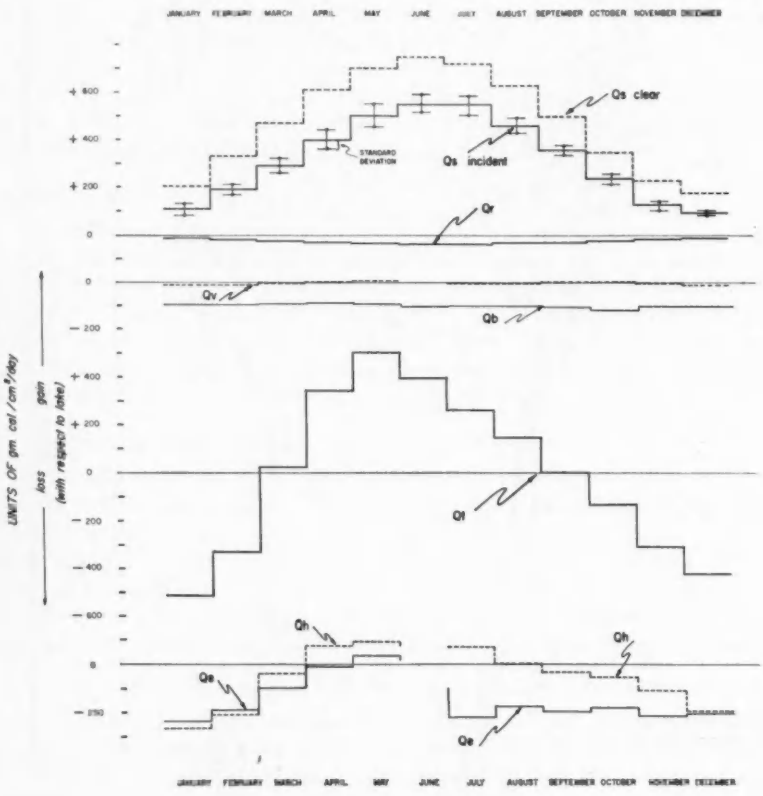

FIG. 2. Terms in the energy budget.

and 10 tenths cloud cover. The value for $(a + be_2)$ was calculated for each of these four cases and a weighted mean used for the calculation of representative values of Q_b for each month.

Air temperatures measured at the 2.5-metre level aboard the *Porte Dauphine* indicate that the 2-metre air temperatures must be much closer to surface water temperatures than to air temperatures measured at land stations. A particular example of this is shown in Fig. 3. There are insufficient data to provide a reliable conversion of land station temperatures to the air temperatures over the water. For this reason, T_2 has been quite arbitrarily taken as:

$$T_2 = T_w - (T_w - T_a)/4 \qquad \ldots (5)$$

This equation seems justified for summer conditions on the basis of the little data available, but does not necessarily hold well for winter conditions.

T_w was taken from Millar's data (Millar, 1952) and T_a (land station data) from the average between Toronto City and Rochester normal air temperatures (U.S. Dept. of Commerce, 1959). See Fig. 4 for T_w and T_a.

The vapour pressure also can be expected to be higher at 2 m over the water than at surrounding land stations. However, since its influence on the calculation of Q_b is probably less marked than that of temperature, no conversion has been attempted.

Months such as January, February, May and June in which $T_w - T_2$ is large have possible errors of ± 20 g-cal/cm^2/day in this present study with less error during months when air and water temperatures are more nearly equal.

Conduction of Sensible Heat (Q_h) and Evaporation (Q_e)

The transfer of heat may be treated similarly to the turbulent transfer of momentum and water vapour. But even if temperature profiles over the lake were known, there is still lack of understanding of details of the mechanism concerning the transfer. For this reason, Q_h is usually related to Q_e by the relationship (Bowen, 1926; Sverdrup *et al.*, 1942):

$$R = Q_h/Q_e = 6.1 \times 10^{-4}\left(\frac{p(T_w - T_a)}{e_w - e_a}\right) \qquad \ldots (6)$$

which is obtained by assuming that the transfer coefficients for heat and water vapour are the same. In equation (6), p is the atmospheric pressure in millibars, and e_w and e_a the corresponding vapour pressures in millibars. For lack of data over the water surface, land station data have been used for T_a and e_a. The monthly mean values of R listed in Table III appear to be large in comparison with those obtained in other studies of over-water conditions (Tabata, 1958; U.S. Geol. Survey, 1954; Sverdrup *et al.*, 1942). On the other hand data obtained at Lake Mead (U.S. Geol. Survey, 1958) suggest that it is immaterial where the air temperature and humidity are measured.

Another error may be due to the use of mean monthly data for computation of the Bowen ratio. A study in Australia (Webb, 1960) indicates the possibility of 5% error due to the fact that the vapour pressure-temperature relation is not linear.

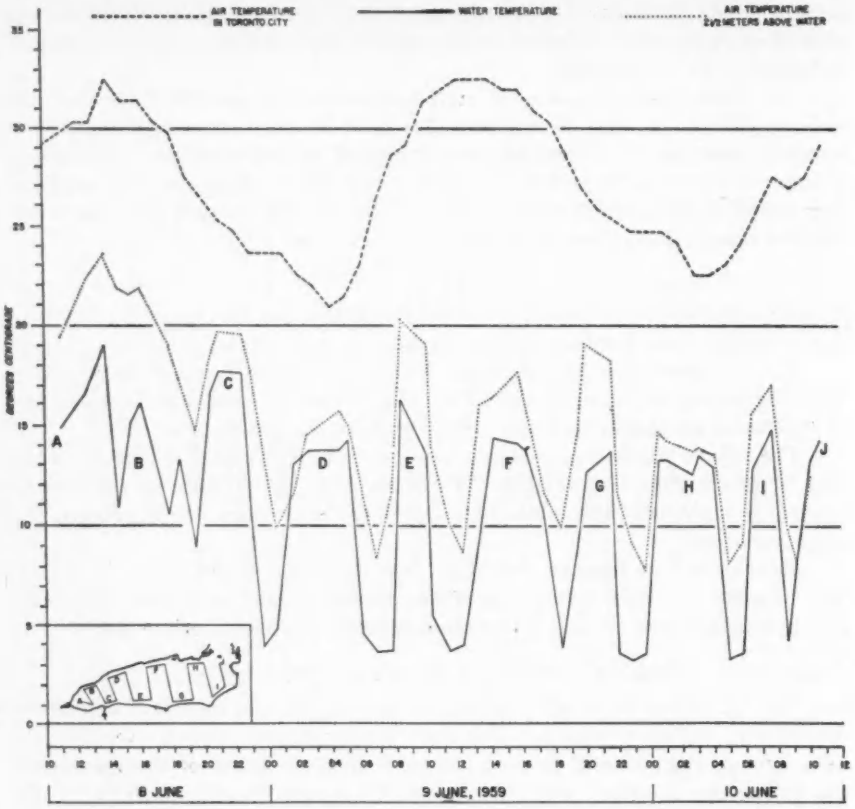

FIG. 3. Comparison of temperatures of air-over-land, air-over-water, and water.

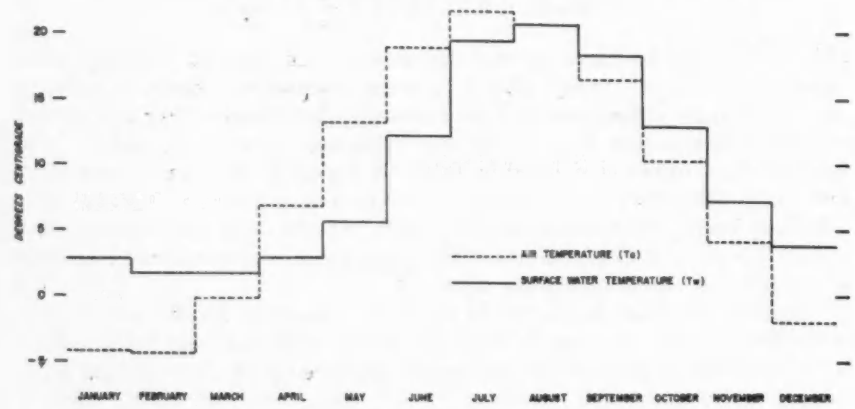

FIG. 4. Long term average monthly surface water temperature (T_w) and land air temperature (T_a). (T_w after Millar, 1952; T_a is the mean of values from Toronto and Rochester).

There appears to be net conduction of energy into the lake from April to July and out of the lake from September to May with maximum lossses from the lake by this process in January and February.

ADVECTIVE TERM AND HEAT STORAGE—Q_v and Q_t

Q_v and Q_t cannot be treated independently since there must be continuity in masses of water entering, leaving, and stored in the lake. From the water balance alone heat is supplied to the lake (or abstracted) according to the following schedule:

Source or sink	Volume symbol	Temperature
Rainfall (total precipitation)	V_p	T_p, wet bulb temperature
Snow melt	V_s	Correction for latent heat of melting (heat loss = Q_m)
Niagara River	V_i	T_i
St. Lawrence River	V_o	At T_o (see Fig. 5)
Lake Ontario watershed	V_r	T_o (see Fig. 5) (in winter at 0°C)
Evaporation	V_e	At surface water temperature T_w

The average values of density d and specific heat c are, closely enough:

$d = 1.0$

$c = 1$ g-cal/cm²/day

Thus we have:

$$Q_v = (V_p T_p + V_i T_i + V_r T_r) - (V_e T_w + V_o T_o) - Q_m \quad \ldots (7a)$$

or:

$$Q_v = Q_i - Q_o - Q_m \quad \ldots (7b)$$

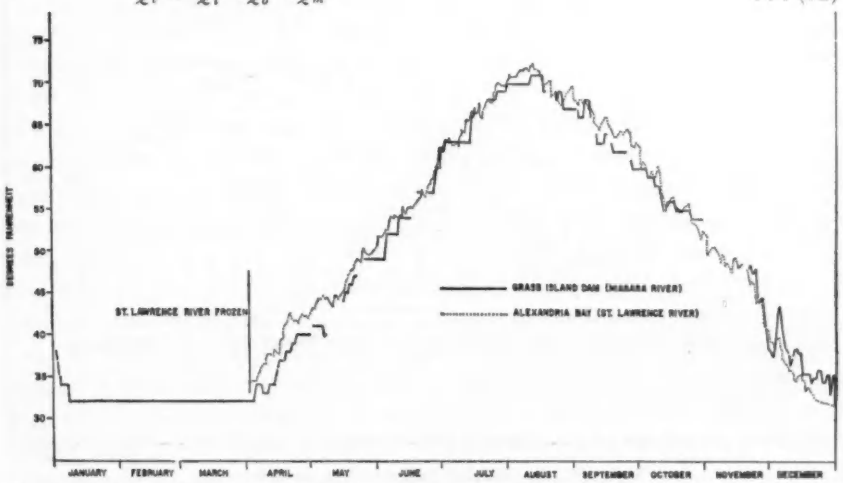

FIG. 5. Inflowing (Niagara River) and outflowing (St. Lawrence River) water temperatures.

If the volume of the lake at the beginning of the month is V_1 and its average temperature T_1, and at the end of the month the values are V_2 and T_2

$$Q_t = (V_2T_2 - V_1T_1) \quad \ldots (8)$$

Since $(V_1-V_2)/V_1$ is about 0.002 for the largest average monthly rise in lake level, very little error is made by using long-term average annual volumes for calculating T_1 and T_2 and thereby as well, Q_t. Monthly change in volume may be easily used, but the error introduced by ignoring it is negligible.

TABLE I. "Advective" terms in the energy budget, in g-cal/cm²/day.

Months	J	F	M	A	M	J	J	A	S	O	N	D
Q_t-Q_s	−1	−1	0	0	+1	+2	0	−3	−6	−2	−2	+1
Q_m	+11	+10	+6	+2	0	0	0	0	0	0	+4	+9
Q_v	−12	−12	−6	−2	1	2	0	−3	−6	−2	−6	−8

It is evident that the water budget terms do not have to be known with a great degree of accuracy for energy budget calculations in such a large lake (see Table I). The water balance of Morton and Rosenberg (1959) has been used in these calculations, including their estimate of V_e, since it is not critical in this calculation.

Q_t as defined in equation (8) has been drawn up from four sets of data, and is shown in Fig. 6. The four sets of data are:

(1) Eight 1958 surveys of Lake Ontario (one survey of 10 stations and seven of about 30 stations);

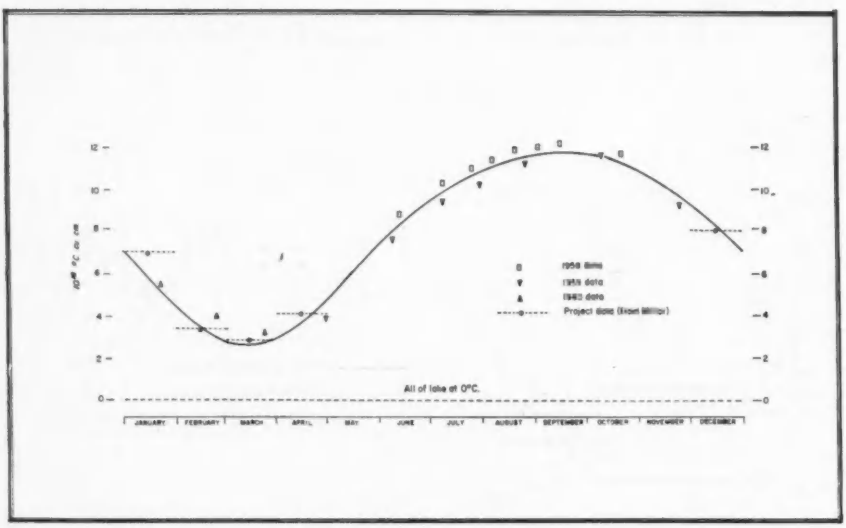

FIG. 6. Average monthly heat content.

(2) Nine 1959 surveys of the lake (one of 44 stations, one of 47 stations and seven of 52 stations);

(3) Average surface temperature transects of Lake Ontario for the months of December through April taken from Millar's (1952) work.

(4) Three winter surveys 1959–60.

In order to estimate winter energy content with the third set of data, two assumptions had to be made. It was assumed that the water had been vertically homogeneous in temperature and that this temperature was uniquely determined by the depth. Millar's temperature transects provide a temperature versus water-depth plot. The lake volume was then divided up into volumes corresponding to several depth intervals, and these volumes, at the temperature given by the temperature-depth graph, provide an estimate of heat content.

The assumption that the water is vertically homogeneous in temperature is supported by Church's work in Lake Michigan (Church, 1942), and by the Lake Ontario winter surveys of 1959–60. In the winter period water temperatures range from 0 to 8°C—a range in which the coefficient of thermal expansion is least for water. This means that the water is close to neutral stability and most easily mixed by winds.

Millar (1952) has noted the control of depth on surface temperature during months of near-neutral stability. This observation prompted the second assumption. If the advective term is small, if vertical mixing is efficient and horizontal mixing limited, and heating (or cooling) uniform over the lake, it is not unreasonable to expect depth control of temperatures in agreement with the observations of 1959–60.

In view of the above limitations, it is believed that the assumptions give reasonable estimates for February and March. The values for December, January and April were used only as guides in drawing the curve of heat content shown in Fig. 6.

The use of only two years' data for plotting the summer heat content and one year's data for the winter, in conjunction with long-term averages of meteorological elements and winter temperatures, should not be thought to imply that the heat content trend does not vary significantly from year to year. Much more work will be required to obtain a satisfactory complete seasonal cycle of heat content and its probable variations with which to correlate the prevailing meteorological conditions.

The time of maximum heat-content lags the time of maximum surface water temperature by about one month, during which time deeper penetration of heat is shown by the continuing rise of temperature at 50 feet (15 m), after surface temperatures have started to decline. Figure 7, showing the seasonal changes in temperature at several levels in the lake, illustrates this phenomenon.

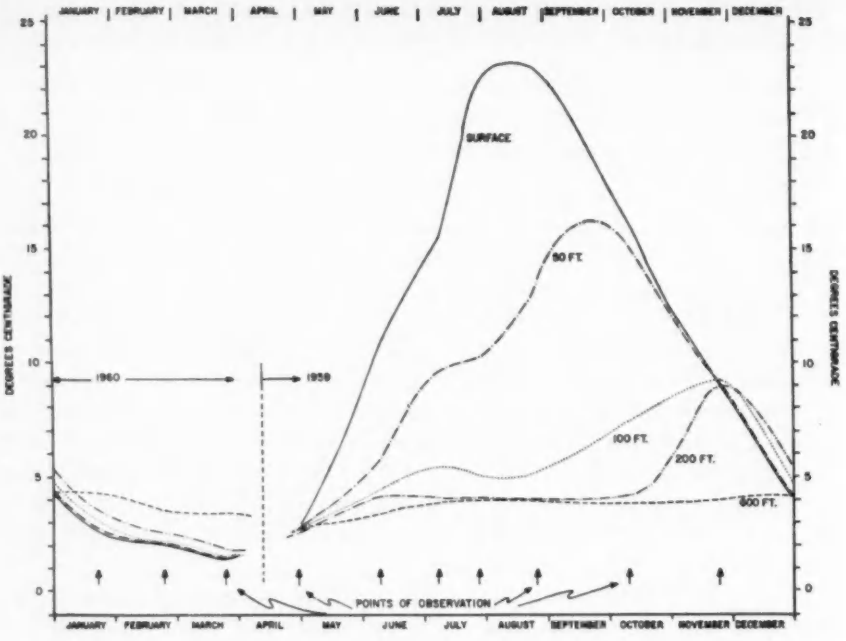

FIG. 7. Seasonal change in average temperature at several levels, 1959–1960.

EVAPORATION

The energy abstracted from the lake by evaporation also removes a certain amount of water from the system. This is given by

$$E = Q_e/dL \qquad \ldots (9)$$

where d is the density of the liquid and L the latent heat of evaporation. L for pure water is given by Sverdrup *et al.* (1942, p. 62):

$$L = 596 - 0.52T_w \text{ calories} \qquad \ldots (10)$$

where T_w is the temperature of the surface water in degrees Centigrade.

The evaporation E in terms of feet of lake level per month appears in Table V, with values from other studies for comparison. Q_e, as it appears in the energy budget, is given in Table II and Fig. 2. For the months of July to February, the evaporation varies little from 200 g-cal/cm²/day, or 0.33 feet per month. From the values of $(e_w - e_a)$ it appears that slight ocndensation may take place in May and June.

TABLE II. The energy budget of Lake Ontario, in g-cal/cm²/day. (See the appendix for explanation of symbols.)

$$Q_s - Q_r - Q_b - Q_e - Q_h + Q_v = Q_t$$

	J	F	M	A	M	J	J	A	S	O	N	D
Q_s	110	190	290	400	500	550	550	460	360	240	130	95
Q_r	13	18	24	28	33	35	36	31	28	22	14	12
Q_b	95	95	90	85	90	100	100	100	105	115	90	90
Q_t	−510	−330	25	345	505	400	265	150	0	−135	−305	−420
Q_v	−12	−11	−6	−2	1	2	0	−3	−6	−2	−6	−8
Q_h	260	210	40	−75	−95	?	−70	0	30	55	110	200
Q_e	240	185	105	15	−35	0?	220	175	190	180	215	205
$(Q_e + Q_h)$	500	395	145	−60	−130	15	150	175	220	235	325	405

TABLE III. Ancillary data. (See the Appendix for explanation of symbols).

	J	F	M	A	M	J	J	A	S	O	N	D
r	.115	.096	.081	.069	.066	.063	.065	.067	.077	.090	.108	.126
T_w °C	2.8	1.7	1.7	2.8	5.6	12.2	19.4	20.6	18.3	12.8	7.2	3.9
T_w-T_a °C	6.9	6.1	1.4	−3.9	−7.6	−6.7	−2.2	0	1.8	2.5	3.0	5.9
RH %	82	80.5	76.5	72	71.5	71	71	72.5	76.5	78.5	80.5	81
e_w–e_a *mb*	3.80	3.35	2.13	0.42	−1.76	−1.28	4.20	6.68	6.66	4.94	3.52	3.80
R	1.11	1.12	0.40	−5.71	2.65	3.21	−0.32	0	0.17	0.31	0.52	0.95

DISCUSSION

ENERGY BUDGET TERMS

Since the advective terms are small, the energy budget is almost independent of water budget determinations when monthly values are considered. The energy content change of the lake is determined therefore, by the imbalance of absorbed short wave-length sun plus sky radiation (i.e., $Q_s - Q_r$) and losses due to evaporation, conduction and net back radiation. The sum $(Q_e+Q_h+Q_b)$ indicates maximum losses in January when the absorbed radiation is close to the yearly minimum value of December (see Fig. 2). This same sum in May shows a slight gain in lake energy due to conduction or convection of energy *into* the lake and condensation of water vapour from the atmosphere—this at a time when the absorbed sun and sky radiation term is approaching the yearly maximum of June and July. The result is maximum heat loss in January, maximum gain in May and near-balanced energy exchange in the months of March and September.

ENERGY BUDGET CALCULATIONS

There are limitations to the accuracy of energy budget calculations as presented in this report. These are enumerated here, with suggestions for future improvement in more detailed applications of the technique. It should be emphasized again that these calculations represent an *average* energy budget. It is clear that substantial differences may occur from year to year in each term for any given month.

The limitation imposed by lack of data and empiricism of the formulae used is most evident in the results for the month of June. In this month the residual $(Q_e + Q_h)$ is +15 g-cal/cm²/day, indicating that there is resultant energy loss from the lake. However, $(e_w - e_a)$ and $(T_w - T_a)$ indicate condensation, and conduction from air to water respectively, both giving energy *gain* for the lake. Fifteen g-cal/cm²/day is well within the possible error of calculations, but the magnitudes of $(e_w - e_a)$ and $(T_w - T_a)$ are such that perhaps an even greater miscalculation might have taken place. The error may be as much as 30 g-cal/cm²/day. Stable conditions in the layer of air over the water make an estimate difficult. This problem cannot be resolved until sufficient meteorological data have been collected over the water surface.

Comparison of the July evaporation values presented in Table V indicates that the value of Q_e for July is high, possibly because of the near-critical value of R. For values of R approaching −1, Q_e becomes large. Thus any small errors in $(T_w\text{-}T_a)$ or $(e_w\text{–}e_a)$ are magnified in the calculation of Q_e. This again casts doubt upon the advisability of using land station data.

Of the terms individually calculated for the energy budget, the value of Q_b is probably the least reliable. The major source of error arises from the need for air temperatures at the 2-metre level in the application of equation (3). Again the need for meteorological data over the lake surface is indicated.

A secondary source of error in the calculation of Q_b might arise from the use of land station cloud height and cloud cover data rather than lake observations in the calculation of $(a + be_2)$ in equation (3). The Malton data are shown in Table IV. For comparison, the average cloud amounts for Rochester airport are also tabulated. As even these two sets of land data differ significantly from

TABLE IV. Comparison of cloud cover at two stations close to Lake Ontario.

	J	F	M	A	M	J	J	A	S	O	N	D
Malton[a]	7.5	7.0	6.6	6.2	5.8	5.7	5.2	5.3	5.3	5.3	7.2	7.4
Rochester[b]	8.1	7.8	7.2	6.7	6.7	5.9	5.5	5.6	5.6	6.1	8.0	8.1

[a]Average for the period 1949 to 1958 inclusive (data supplied by the Meteorological Branch, Canada Department of Transport).
[b]18-year average (U.S. Weather Bureau, Publication No. 35).

one another, it will be necessary as well to determine lake cloud cover directly, and so find how it is related to land cloud cover. The lake produces its own cloud regime, the likelihood being that it is cloudier over the lake than on surrounding land in winter and less cloudy in summer.

The question of cloud cover is even more important in the determination of the incident solar radiation. Cloud cover reduces the total possible radiation (with continuously clear skies) by 50% in winter and 20 to 30% in summer. A one-tenth difference in cloud cover for a given month will alter the flux of incident radiation in winter by 20 and in summer by 80 g-cal/cm²/day.

It will also be necessary to have direct incident radiation measurements on the lake for periods even as long as one month. The location of such instruments

must be carefully planned to allow for likely disparity of land and lake cloud cover.

Lake ice cover in winter has not been considered in the calculations of this report, since Lake Ontario has substantial ice cover only in the outlet basin, which has been excluded. It affects both Q_b and Q_r. Usually, since ice surface temperatures can become colder than water surface temperatures, the Q_b, as

TABLE V. Evaporation of Lake Ontario, in feet of lake level per month. (1 foot = 0.305 m).

Method	Water budget		Mass transfer					Energy budget
Reference	Hunt 1959	Morton & Rosenberg 1959	Freeman 1926	Hunt 1959	Kohler 1959	Snyder 1960	Bruce & Rodgers 1959	This study
Jan.	.20	.27	.22	.23	.26	.26	.33	.41
Feb.	.10	.19	.22	.18	.21	.23	.27	.29
Mar.	.06	.07	.13	.18	.18	.14	.19	.17
Apr.	.03	.07	.09	.07	.08	.05	.05	.02
May	.02	.04	.02	0	0	−.05	−.11	−.06
June	−.02	.02	.09	.01	.02	.01	−.05	0
July	.09	.15	.31	.16	.19	.19	.24	.38
Aug.	.26	.33	.43	.21	.23	.33	.41	.29
Sept.	.32	.35	.38	.32	.32	.35	.53	.33
Oct.	.37	.38	.36	.27	.27	.31	.43	.31
Nov.	.34	.37	.20	.23	.22	.22	.33	.36
Dec.	.32	.37	.20	.20	.24	.25	.14	.35
Totals	2.09[a]	2.61	2.65	2.06	2.22[b]	2.28	2.76	2.85

[a]With the precipitation ratio $P_w/P_l = 1$, the annual total is 2.71 feet.
[b]Pan evaporation average of 6 stations (Kohler, 1959) gives an annual total of 2.39 feet.

calculated for this report, would be larger than the true back radiation term if ice cover were extensive.

The albedo of ice and snow-covered ice is much greater than that of a water surface. In respect of Q_r, where:

$$Q_r = r\,Q_s \qquad \ldots (11)$$

(r being the albedo) a new snow surface can give rise to an r as high as 0.80.

The lowest average surface water temperatures are given for the months of February and March, and ice cover would affect Q_r for these months. The lowest monthly average surface temperatures are 35°F (1.7°C), with the highest temperatures in mid-Lake (Millar, 1952). Thus it appears that a great deal of ice cannot occur. It is likely to be restricted to shallow waters (shorelines and shallow basins) and the deep waters are probably always free of ice. It is estimated that 10% coverage at the shoreline would be a maximum in the most severe winter. This ice cover might have an albedo (r) of 0.50. Thus, the effective r for February for the whole lake (excluding the outlet basin) would be 0.14 rather than the 0.10 used. Q_r would then be 28 instead of 20 g-cal/cm²/day. This is considered an upper limit to the possible error in Q_r introduced by neglecting ice cover.

Aerial ice reconnaissance was started by the Meterological Branch of the Canada Department of Transport in January, 1960 and this will provide data on all the lakes for such problems in future.

Since the energy storage term is a major term in the energy budget, attention must be paid to the quality of surveys designed to provide energy content data for detailed study of specific periods of time. For example, small changes in the calibration of the bathythermographs of the order of one tenth of a centigrade degree can change Q_t by 30 g-cal/cm²/day. Use of reversing thermometers to check bathythermograph readings is necessary in order to reduce this error. An alternative is to use a more sensitive recorder such as the TPR (Temperature Profile Recorder) instrument, described in the Lake Hefner study (Anderson, 1954).

Another possible error in Q_t may result from the fact that the surveys are quasisynoptic. The 1959 surveys required about 40 hours to complete. The presence of an internal seiche may cause apparent heat content values to be too high or too low depending on the state of the seiche, the direction of the wind and the pattern of the stations chosen. An estimate can be made of the magnitude of the error incurred by neglecting internal seiches, the effect being greatest during the summer stratification. A uninodal seiche in a simplified two-layer system, with an epilimnion 50 feet (15 m) deep at 20°C and a hypolimnion at 4°C, has a period of about 12 days in Lake Ontario. If the internal seiche has a maximum full amplitude of 10 feet (3 m) at each end of the lake, if one of the surveys defining the heat content at the end of a one-month period takes 2 days (travelling from one end of the lake to the other), and if the time of this survey coincides with the time of maximum vertical movement of the temperature boundary, the apparent Q_t could differ from the true Q_t by 20 g-cal/cm²/day for 2 surveys one month apart.

The evaporation determined from energy budget calculations follows the seasonal trend obtained by other methods (see Table I); that is, appreciable evaporation from July to February, less evaporation in March, and little evaporation or slight condensation in April, May and June but the annual total evaporation of 2.8(4) feet (0.87 m) is the highest of all the estimates.

This estimate might be expected to be high in view of the possible errors considered above. The evaporation for June was taken as zero when the sign of $(e_w - e_a)$ and the results of some of the other studies suggest that slight condensation takes place. This might account for an over-estimate of about 0.03 feet (0.01 m). The energy budget value for July, as remarked upon above, is higher than those for other studies and may be due to the sensitivity of equation (2) for the critical value of the Bowen ratio (R approaching −1). The values from other studies suggest that E for July by the energy budget technique may be 0.10 feet (0.03 m) too high. These two possible positive errors of 0.1 would bring the annual total down to 2.7 feet (0.82 m), in approximate agreement with the higher water-budget and mass-transfer estimates. It must be emphasized, however, that the probable error of this average heat budget, which is certainly

more than 10%, and the magnitude of likely yearly variations from it, cannot yet be stated with any statistical certainty.

The particularly low values include Hunt's (1959) water budget calculation, and Hunt's (1959) and Kohler's (1959) mass transfer calculations. If Hunt's water budget values are recalculated on the basis of a ratio of 1.00 for precipitation-over-water to precipitation-over-land, the total annual evaporation becomes 2.71 feet (0.83 m). Hunt employed ratios of 0.59 to 0.92 with an annual average ratio of 0.79. Present evidence from northern Lake Michigan (Blust and DeCooke, 1960) is that seasonal differences may be as high as 10%, but the annual totals are nearly the same (±2%). There is no guarantee that this applies to all regions of the Great Lakes, but it does suggest that a 20% difference in annual total precipitation is probably excessive.

Hunt's mass transfer calculation would be revised upward if two pieces of data which he used were reconsidered. There is a fairly large discrepancy between the monthly average surface temperatures recorded by Millar (1952) and those used by Hunt for the winter months. Four surveys carried out by the *Porte Dauphine* on the pattern shown in Fig. 1 gave the following mean surface temperatures and temperature ranges. The monthly average temperatures given by Hunt and Millar are shown for comparison. These temperatures confirm Millar's data.

Date	Mean surface Temperature	Temperature Range	Mean monthly temp. Hunt	Millar
	°F	°F	°F	°F
Dec. 16–21, 1959	40.1	43.9 to 35.6	34	39
Jan. 20–24, 1960	36.7	40.2 to 32.3	32	37
Feb. 22–25, 1960	35.6	38.5 to 32.2	32	35
Mar. 23–26, 1960	34.3	36.0 to 32.4	35	35

Hunt recognized the need to adjust winds measured over land for application over the water. He extrapolated from land station data using information obtained at Lake Okeechobee, Florida. This information led Hunt to increase land wind data 5 to 35% to give over-water winds. An analysis of ship records provided by Lanczi (see Bruce and Rodgers, 1959) suggests that this increase should be between 55 and 85%. A recalculation incorporating Millar's surface temperatures and the larger over-water winds was carried out (Bruce and Rodgers, 1959); this, shown in Table V, gives the greater annual total of 2.7(6) feet (0.84 m). This estimate still contains the uncertainty of the use of land station data for the vapour pressure of the air over the water.

Kohler's mass transfer calculations are based on land station data and a formula developed in the Lake Hefner study. Disparity in the sizes of Lakes Hefner and Ontario probably invalidates the formula used, since a large lake produces its own "climate". This also may be the reason for Snyder's (1960) low value. The lake affects the temperature and water vapour content of the air masses flowing over the lake. Wind profiles over the lake differ from those over land due to different stability conditions and different surface roughness

parameters. Cloud development over the lake is different from cloud development over land. Each of these meterological elements must be determined in order rigorously to apply present techniques for evaluating the energy budget of lakes as large as any of the Great Lakes.

Land stations provided the climatological data for this report. There are few climatological data available yet from the Lakes and modification of the land station data used for this study was therefore rather arbitrary.

Meteorological stations placed on exposed points of land and on islands provide useful information. Data provided by recording or by telemetering weather buoys in open waters could provide systematic climatological data which would be more easily treated than the data presently being collected by moving ships.

Finally, it is hoped that further research into the physics of interaction of the atmosphere and lake surface will reduce the empiricism of energy exchange relationships and improve the accuracy of their assessment.

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APPENDIX: List of symbols

Symbol	*Description*
a	parameter defined by equation 4a.
b	parameter defined by equation 4b.
C	cloud cover.
d	density.
e_2	vapour pressure of water in the air at 2.0 m above the water surface.
e_w	vapour pressure of saturated air at the temperature, T_w.
E	mass of water evaporated.
h	cloud height.
L	latent heat of vaporization of water.
P_w	precipitation over water.
P_l	precipitation over land.
Q_b	net back radiation.
Q_e	energy involved in evaporation.
Q_h	conduction of sensible heat to the atmosphere.
Q_i	energy flow of water masses entering the lake.
Q_m	heat loss involved in converting snow at 0°C. to water at 0°C.
Q_o	energy flow of water masses leaving the lake.
Q_r	reflected solar radiation.
Q_s	solar radiation incident to water surface.
Q_t	energy storage of the body of water.
Q_v	net advected energy.
r	albedo of the water surface.
R	Bowen ratio defined in equation (2).
T_a	air temperature measured at a land station.
T_w	surface water temperature.
T_2	air temperature at 2.0 m above the water surface.
T_p, T_o, T_1 and T_2, V_e, V_i, V_o, V_p, V_r, V_s, V_1, and V_2 are all defined in the text, page 625.	

NOTES

Muscle Proteins of Pacific Salmon (*Oncorhynchus*) I. A Note on the Separation of Muscle Proteins Soluble in Low Ionic Strength Salt Solutions

Whole extracts of fish muscle proteins soluble in salt solutions of low ionic strength have been studied by several groups of investigators. Connell (1953) and Nikkilä and Linko (1955) have between them carried out a general survey of the electrophoretic properties of muscle proteins of fishes of various biological types, representing a total of about 25 species. Hamoir (1951, 1954, 1955a, b) and Henrotte (1952, 1954, 1955) have studied the carp muscle proteins extensively, and Dingle and associates (1955) the Atlantic cod (*Gadus callarias* L.) by electrophoretic methods.

The Pacific salmon (genus *Oncorhynchus*), however, have not been studied in this respect. The present communication describes the separation of muscle proteins of Pacific coast spring salmon (*O. tshawytscha*) by the use of diethylaminoethyl (DEAE) cellulose columns and also some electrophoretic studies of the proteins.

The protein extract was prepared by chopping the muscle tissue into small pieces and homogenizing in a Waring Blendor with 10 volumes of a 0.05 ionic strength phosphate buffer of pH 7.5, similar to that used by Connell (1953). All operations were carried out at 0°C and all glassware was pre-chilled. The blendor jar was loosely fitted with a plexiglass baffle plate extending just below the surface of the liquid to eliminate the vortex (Dyer *et al.*, 1950). Homogenization was carried out for ten 10-second intervals spaced sufficiently apart to allow the larger particles to settle towards the blades of the blendor. The blendor was operated at its high-speed position with a variac setting of 50 volts. The homogenate was centrifuged at 3000 g for 30 minutes in a Servall Type RC-2 automatic refrigerated centrifuge and the supernatant stored at 0°C. This protein solution was dialyzed exhaustively against the appropriate buffer at 0°C and centrifuged at 10,000 *g* for column chromatography and at 144,000 *g* for electrophoresis.

DEAE cellulose column methods have been used for the purification from lingcod (*Ophiodon elongatus*) muscle of a variety of enzymes (Tomlinson, 1959; Tarr, 1959; Martin and Tarr, 1961). In all these instances a convex type of gradient elution was used. In view of the success achieved in these experiments, whole extracts of salmon muscle proteins were separated by means of DEAE cellulose columns (Fig. 1). In this case, however, a concave upward type of

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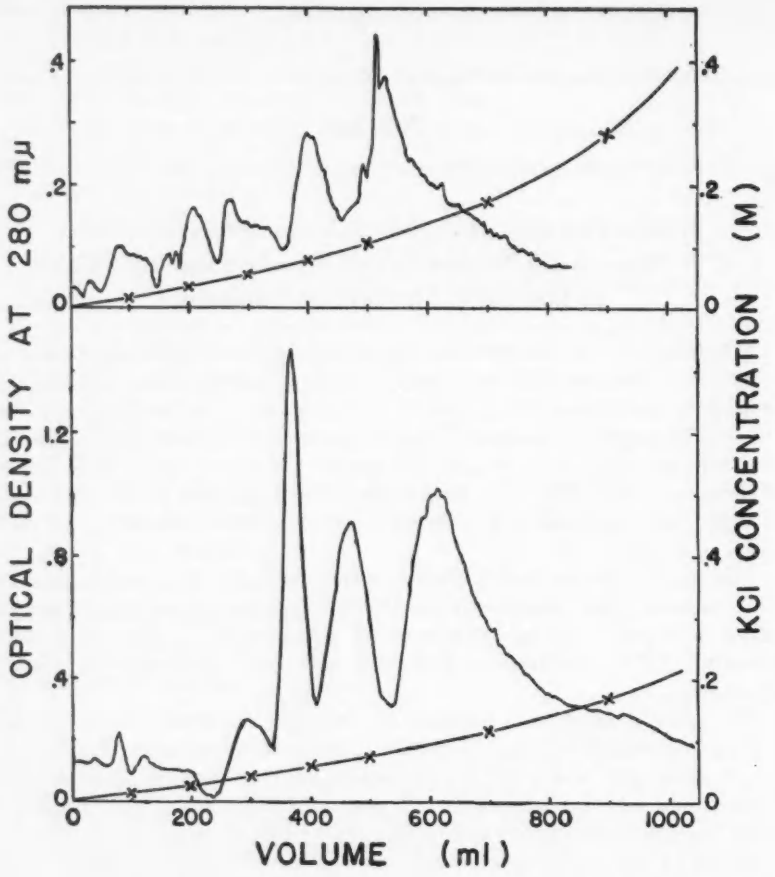

FIG. 1. DEAE column separation of salmon muscle proteins soluble in low ionic strength salt solutions. The spring salmon weighing approximately 5 lb each were caught by troll at sea and held for 8 hr in a tank under anaesthesia (tricaine methanesulphonate). The fish were then killed and filleted immediately. A portion of the fillets was extracted immediately and the remainder were sealed in polyethylene bags and stored at −35°C.

Upper. 9.0 g of DEAE Type 20, capacity 0.85 meq/g (Carl Schleicher and Schuell Co. Keene, New Hampshire) was packed in a 1.4-cm diameter column to a height of 45 cm in 0.001*M* Tris-HCl pH 8.5, and washed with several bed volumes of this solution. The protein extract (258.8 mg protein) was applied to the column and eluted by concave upward type of gradient with increasing concentrations of Tris pH 8.5 and KCl at a temperature of 0°C. The crosses represent the potassium chloride concentration gradient. Five-ml fractions were collected by a G.M.E. Model 10 Fraction Collector.

Lower. 13.0 g of DEAE packed to a height of 65 cm in a column of the same diameter as above and in a similar manner. Protein extract (573 mg protein) was applied and eluted as before.

gradient elution was used in order to obtain a more gradual increase in the salt concentration during the beginning of the elution. Sudden increases in concentration as would be expected by stepwise elution were avoided since such techniques may lead to artifactitious peaks (Sober and Peterson, 1958). Preliminary experiments indicated that at pH's below 5.0 there was considerable precipitation of the protein extract, while at 7.5 the protein was not retained on the column. In contrast, the water-soluble lingcod muscle proteins purified initially by ammonium sulphate precipitation were retained at pH 7.0 (Tomlinson, 1959; Tarr, 1959; Martin and Tarr, 1961). At pH 8.5, however, the salmon proteins remained soluble and were retained on the DEAE column. Elution with increasing concentrations of potassium chloride and Tris-HCl (tris(hydroxymethyl)aminomethane) resolved the proteins into at least ten components (Fig. 1, upper). Storage of the protein extract at −35°C caused some precipitation of the small components eluting earlier when compared with the larger components coming off the column later (Fig. 1, lower). The use of a longer column (Fig. 1, lower) increased the resolution somewhat. Column chromatography, therefore, provides a simple technique of high resolution for the separation of fish muscle proteins soluble in low ionic strength salt solutions.

Electrophoresis of salmon muscle proteins using a Spinco Model H Electrophoresis–Diffusion apparatus at pH 6.5, ionic strength 0.15 (0.1*M* with respect to sodium chloride) phosphate buffer showed little tendency for the proteins to migrate. Under similar conditions, the seven identifiable protein components from post-rigor cod muscle extractable with low ionic strength salt solutions show a range of values from 8.4×10^{-5} to 0.82×10^{-5} cm^2 $volt^{-1}$ sec^{-1} (Dingle *et al.*, 1955). This indicates considerable differences in the properties of the proteins between the salmon and the cod. At pH 8.0 phosphate buffer of ionic strength 0.05 the salmon proteins showed the presence of seven components after a 6-hr run. The mobility values were found to fall within the limits of -0.95×10^{-5} to -2.85×10^{-5} cm^2 $volt^{-1}$ sec^{-1}. Runs were not made at pH's lower than 6.0 since considerable precipitation was obtained.

These studies are being continued and further details of these experiments will be reported at a later date.

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Temperature and the Biochemical Processes Occurring During Rigor Mortis in Cod Muscle[1]

The rapid biochemical changes which take place in muscle immediately post-mortem, especially the processes which occur during the onset and resolution of rigor mortis, have been widely studied in mammalian muscle. This work has been extensively reviewed by Bate-Smith (1948) and Whitaker (1959). Commercial fish species, however, have received little attention. Some early investigations were carried out on glycogen and lactic acid relations in trawled and hand-lined haddock, hake, cod and sculpin (Ritchie, 1926; MacLeod and Simpson, 1927; Leim, *et al.*, 1927; Macpherson, 1932; and Sharp, 1934). These workers showed that struggling reduced the muscle glycogen with accumulation of lactic acid, and concluded that the time of onset, the degree and duration of rigor mortis were dependent upon a number of factors, the most important being the method of catching. Later work has shown that an enzymic breakdown of adenosine triphosphate (ATP) by actomyosin ATPase or apyrase occurs in fish muscle (Partmann, 1954; Golovkin and Pershina, 1957), but apart from a few observations on frigate mackerel by Amano *et al.* (1953), no published data appear to exist on the deamination of adenosine nucleotides with the liberation of ammonia.

The interrelation of these biochemical processes associated with rigor mortis in fish muscle has not been established as yet. To elucidate these relations, the rate and extent of the breakdown of glycogen to lactic acid, the dephosphorylation of ATP, the deamination of adenosine nucleotides to inosine nucleotides with the liberation of ammonia, and the time to onset of rigor have been studied in Atlantic cod (*Gadus morhua*) muscle at various temperatures.

Rested cod held in a large aquarium at the laboratory were used. Struggling normally associated with death was reduced to a minimum by anaesthetizing the fish in a 0.1% solution of MS222 (Tricaine methanesulphonate; Sandoz Pharmaceuticals) prior to filleting. The metabolites were extracted immediately by homogenizing the muscle with six volumes of ice-cold 3% perchloric acid, followed by filtration and washing of the residue with additional 3% perchloric acid.

The changes in ATP (7-minute acid-labile phosphorus (LePage, 1949)) and in ammonia content of rested cod muscle held at temperatures of 0, 9, and 25°C after death are shown in Fig. 1. The onset of rigor occurred much earlier at the higher temperatures; post-mortem times at 0, 9, and 25°C were 12, 6, and ½ hours respectively. Similar times to onset of rigor were found in a more extensive investigation of the effect of temperature and other factors influencing rigor in cod fillets (Dyer and Fraser, 1961). In eight samples of aquarium-held cod, the initial ATP content ranged from 27 to 40 mg P per 100 g muscle. This corresponded to an average of 5.2 micromoles ATP per g, which compared favourably with the value of 5.34 reported by Jones and Murray (1960) in rested cod muscle.

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During the pre-rigor period the ATP disappeared rapidly, the process occurring more quickly at the higher temperatures. A similar temperature effect was observed by Saito and Arai (1957) who reported a more rapid dephosphorylation in carp muscle held at 16°C than at 0°C. Deamination of the adenosine nucleotides to inosine nucleotides with the liberation of ammonia accompanied the dephosphorylation. This process also occurred very much faster at the higher temperatures. Initial ammonia content ranged from 2.7 to 4.5 mg N per 100 g muscle, and increased to 10 to 11 mg N per 100 g during the resolution of rigor. The dephosphorylation and deamination occurred simultaneously, as has been reported for rabbit muscle by Bendall and Davy (1957). Deamination was substantiated by a change in the ultraviolet absorption maximum of the extract from 258 to 248 mμ, characteristic of adenosine and inosine nucleotides respectively. The rates of dephosphorylation and of deamination at 0°C observed in cod muscle are considerably slower than those found in trout muscle by Saito *et al.* (1959). This may indicate that the enzyme activity is less in the more sluggish cod.

The effect of temperature on the rate of glycogen depletion and of lactic acid formation is shown in Fig. 2. Initial glycogen values for rested cod from the aquarium were usually less than 0.1%, and the amount of lactic acid formed rarely exceeded 0.2%. In contrast, Sharp (1934) found initial glycogen contents of 0.6 to 0.85% in resting haddock; no reliable figures are available for cod muscle. The low glycogen values are probably due to the starved or semi-starved condition of the fish, since they were held at a water temperature near 0°C where feeding does not occur (MacKenzie, 1938). Thus, little muscle glycogen is available for degradation to lactic acid, and consequently the ultimate pH values during rigor remain near 7 (the so-called "alkaline" rigor). In the majority of these cod, the pH was initially 7.2 to 7.5, and it did not fall below an ultimate value of 6.9 as rigor was resolved. Similar high ultimate pH values were reported by Love (1958) with cod starved for long periods. However, Black *et al.* (1960) did not find the expected lowered muscle glycogen after starvation of trout for 3 to 7 days.

In Fig. 2, the very marked effect of temperature on the rate of glycolysis is illustrated. Lactic acid formation continued actively beyond the point of onset of rigor at each of the three temperatures investigated, 0, 9 and 25°C. At 25°C lactic acid formation had not reached the maximum even at 4 hours, whereas full rigor had been established at between 40 minutes and 1 hour. These results do not support the conclusion of Tomlinson *et al.* (1961) that maximum formation of lactic acid has been completed by the time of full rigor at temperatures near 20°C in unexercised rainbow trout (*Salmo gairdneri*) and Pacific coast starry flounder (*Platichthys stellatus*).

During this work, a few samples of otter-trawled cod and haddock, quickly frozen in brine after catching, were found to contain almost no glycogen. It was also observed that very rapid glycolysis, accompanied by dephosphorylation and deamination, occurred during thawing of a sample of rested cod muscle frozen in the pre-rigor state.

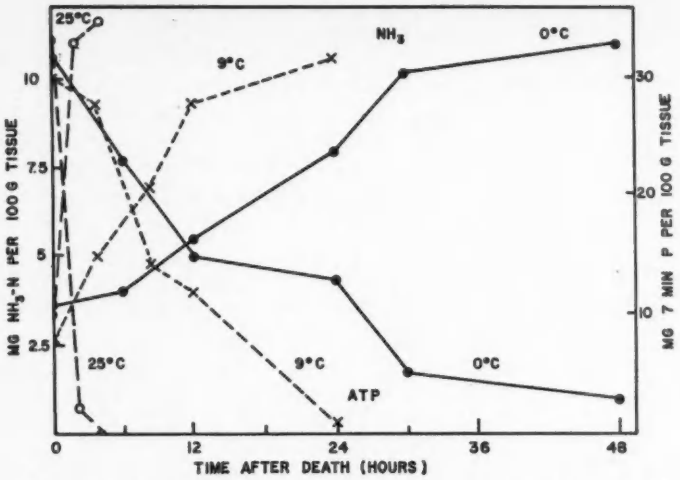

FIG. 1. ATP and ammonia changes in rested cod muscle at 0, 9, and 25°C.

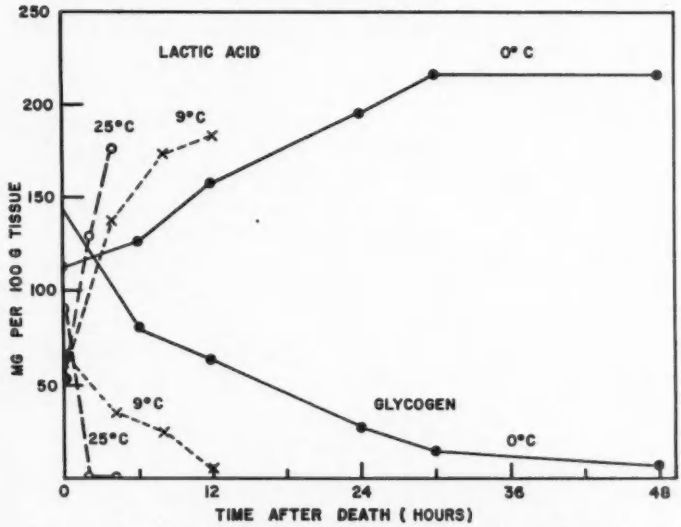

FIG. 2. Glycogen and lactic acid changes in rested cod muscle at 0, 9, and 25°C.

In conclusion, temperature markedly affected the rate of glycolysis in cod muscle; dephosphorylation and deamination of the adenine nucleotides occurred simultaneously with glycolysis. These processes were complete in about 30 hr at 0°C, 12 hr at 9°C, and in just over 2 hr at 25°C. In view of the increasing amounts of pre-rigor fish being processed industrially, the importance of these

changes associated with rigor mortis is becoming clearer. Our increasing knowledge should lead to the solution of some of the difficulties encountered in processing very fresh fish.

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